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

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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. haschelanus (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 Nicobars, 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. Nevertheless, 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 Oclocyozinae 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 deferred 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 Sunda-land (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. hasceanus* 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. hasceanus*, 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-
**Minervarya andamanensis** 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 narrowing 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 | Accession Number  | Reference               |
|-----|-------------------------|---------------------|-------------------|-------------------------|
| 1   | *Minervarya andamanensis* | n.a.                | AB277300          | Suwannapoom et al. 2017 |
| 2   | *Minervarya andamanensis* | India: Andaman Island | AB277321          | Present study           |
| 3   | *Minervarya andamanensis* | India: South Andaman: Mt. Harriet National Park | AB277322          | Present study           |
| 4   | *Minervarya andamanensis* | India: South Andaman: Chidiya Taapu | AB277323          | Present study           |
| 5   | *Minervarya andamanensis* | India: South Andaman: Chidiya Taapu | AB277324          | Present study           |
| 6   | *Minervarya andamanensis* | n.a.                | AB277325          | Present study           |
| 7   | *Minervarya andamanensis* | India: Little Andaman  | AB277326          | Present study           |
| 8   | *Minervarya andamanensis* | Thailand: Phra Nakhon, Thong Pha Phum | AB277327          | Present study           |
| 9   | *Minervarya andamanensis* | Myanmar: Bago, Dawei | AB277328          | Present study           |

**List of DNA sequences included in the phylogenetic study.**

**Table 1.** List of DNA sequences included in the phylogenetic study.
| S.N | Taxa                | Collection Locality     | Voucher No.       | Accession Number | Reference              |
|-----|---------------------|-------------------------|------------------|------------------|------------------------|
| 17  | M. muangkanensis    | Myanmar: Bago, Dawei    | USNM:Herp:587073 | MG935779         | n.a.                   |
| 18  | M. muangkanensis    | Myanmar: Tanintharyi, Yeybu village | USNM:Herp:586873 | MG935780         | n.a.                   |
| 19  | M. muangkanensis    | Myanmar: Tanintharyi, Yeybu village | USNM:Herp:586874 | MG935781         | n.a.                   |
| 20  | M. muangkanensis    | Myanmar: Tanintharyi, Yeybu village | USNM:Herp:586875 | MG935782         | n.a.                   |
| 21  | M. muangkanensis    | Myanmar: Tanintharyi, Yeybu village | USNM:Herp:586876 | MG935783         | n.a.                   |
| 22  | M. muangkanensis    | Myanmar: Tanintharyi, Yeybu village | USNM:Herp:586878 | MG935784         | n.a.                   |
| 23  | M. muangkanensis    | Myanmar: Tanintharyi, Yeybu village | USNM:Herp:586879 | MG935785         | n.a.                   |
| 24  | M. muangkanensis    | Myanmar: Ayeyarwady, near Mwe Hauk village | CAS 208016       | MK621439         | n.a.                   |
| 25  | M. muangkanensis    | Myanmar: Ayeyarwady, near Mwe Hauk village | CAS 208033       | MK621440         | n.a.                   |
| 26  | M. muangkanensis    | Myanmar: Ayeyarwady, near Kyanigan | SMF 103782       | MK621441         | n.a.                   |
| 27  | M. muangkanensis    | Myanmar: Ayeyarwady, near Kyanigan | SMF 103787       | MK621442         | n.a.                   |
| 28  | M. muangkanensis    | Myanmar: Ayeyarwady, Kan Ywa to Negwesaung | SMF 103790       | MK621444         | n.a.                   |
| 29  | M. muangkanensis    | Myanmar: Ayeyarwady, Kan Ywa to Negwesaung | SMF 105012       | MK621446         | n.a.                   |
| 30  | M. muangkanensis    | Myanmar: Ayeyarwady, Kan Ywa to Negwesaung | SMF 105013       | MK621447         | n.a.                   |
| 31  | M. muangkanensis    | Myanmar: Ayeyarwady, Kan Ywa to Negwesaung | SMF 105012       | MK621446         | n.a.                   |
| 32  | M. muangkanensis    | Myanmar: Ayeyarwady, Kan Ywa to Negwesaung | SMF 105013       | MK621447         | n.a.                   |
| 33  | M. agricola        | India: Karnataka: Mudigere | BNHS 4651        | AB488895         | AB488872              |
| 34  | M. agricola        | India: South Andaman: Chidiya Taapu | SDBDU 2019.3986  | ON009967         | n.a.                   |
| 35  | M. agricola        | India: South Andaman: Sippi Ghat | SDBDU 2019.4027  | ON009968         | n.a.                   |
| 36  | M. agricola        | India: Middle Andaman: Rangat | SDBDU 2019.4054  | ON009969         | n.a.                   |
| 37  | M. asmati          | India: Assam            | n.a.             | AB488900         | AB488877              |
| 38  | M. chiangmaiensis  | Thailand: Chiang Mai: Omkoi | KIZ024057        | KX834135         | n.a.                   |
| 39  | M. tenasiensis     | India: Assam            | AB488900         | AB488877         | AB489016              |
| 40  | M. greensis        | Sri Lanka: Hakgala      | MNHN 2000.617    | AB488891         | AB488868              |
| 41  | M. kirtisinghei    | Sri Lanka: Hakgala      | MNHN 2000.620    | AB488890         | AB488867              |
| 42  | M. brevipalmata    | India: Kerala: Kadalav | SDBDU 2011.1048  | MZ156230         | n.a.                   |
| 43  | M. goemchi         | India: Goa: Surli       | ZSI/WRC/A/2017   | MG800343         | n.a.                   |
| 44  | M. mysorensis      | India: Karnataka: Kudremukh | BNHS 4653 / 4654 | AB488898         | AB488875              |
| 45  | M. kerakensis      | India: Kerala: Kadalav | SDBDU 2011.1048  | MZ156230         | n.a.                   |
| 46  | M. nilagirica      | India: Madikeri         | BNHS 4646        | AB488896         | AB488873              |
| 47  | M. kalinga         | India: Odisha: Barbara Reserve Forest | SDBDU 2015.308  | MZ156316         | n.a.                   |
| 48  | M. cephi           | India: Maharashtra: Amboli | ZSI/WGRC/V/A/938 | KY44708          | n.a.                   |
| 49  | M. kado            | India: Kerala: Thvalakuzhipara | ZSI/WGRC/V/A/940 | KY44712          | n.a.                   |
| 50  | M. manoharani      | India: Kerala: Chathankod-Bonnacad | ZSI/WGRC/V/A/945 | KY44713          | n.a.                   |
| 51  | M. neilcoxi        | India: Kerala: Parambikulam | ZSI/WGRC/V/A/951 | KY447318        | n.a.                   |
| S/N | Taxa                        | Collection Locality | Accession Number | Reference                                      | FLI–IV                        |
|-----|-----------------------------|---------------------|------------------|------------------------------------------------|-------------------------------|
| 52  | *M. rufescens*              | India: Padil: Mangalore | AB488874        | Hasan et al. 2014; Kotaki et al. 2008          |                               |
| 53  | *M. marathi*                | India: Maharashtra: Pune, Bhamburde | AB530602 | Phuge et al. 2019                             |                               |
| 54  | *M. sahyadris*              | India: Karnataka: Mangalore | AB488877       | Garg and Biju 2021                             |                               |
| 55  | *M. gomantaki*              | India: Codal village | VN1005          | Dinesh et al. 2015                            |                               |
| 56  | *M. krishnan*               | India: Karnataka: Jog Falls | MZ156034       | Garg and Biju 2021                             |                               |
| 57  | *M. syhadrensis*            | India: Karnataka: Mudigere | MZ156093       | Garg and Biju 2021                             |                               |
| 58  | *M. nepalensis*             | Nepal: Chitwan       | AB488889        | Kotaki et al. 2010                            |                               |
| 59  | *M. pentali*                | India: Kerala: Nedumbaserry | MZ156072       | Garg and Biju 2021                             |                               |
| 60  | *F. limnocharis*            | Indonesia: Bogor     | AB488886        | Kotaki et al. 2010                            |                               |
| 61  | *F. orissaensis*            | India: Odisha        | AB488887        | Kotaki et al. 2010                            |                               |
| 62  | *S. dobsonii*               | India: Bajipe        | AB488888        | Kotaki et al. 2010                            |                               |
| 63  | *S. pluvialis*              | Sri Lanka            | AB488889        | Kotaki et al. 2010                            |                               |
| 64  | *E. cyanophlyctis*          | India               | AB488900        | Kotaki et al. 2010                            |                               |
| 65  | *E. hexadactylus*           | India: Mudigere      | AB488901        | Kotaki et al. 2010                            |                               |
| 66  | *H. crassus*                | Sri Lanka            | AB488902        | Kotaki et al. 2010                            |                               |
| 67  | *H. tigerinus*              | India: Mangalore     | AB488903        | Kotaki et al. 2010                            |                               |
| 68  | *N. ceylonensis*            | Sri Lanka            | AB488904        | Kotaki et al. 2010                            |                               |
| 69  | *L. laticeps*               | Malaysia: Kuala Lumpur | AB488905       | Kotaki et al. 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), 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), FL3,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).
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 Tvr) 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, UBF 99) lineage in the *M. andamanensis* species group (Garg and Biju 2021). It also formed a highly supported (BPP 100, UBF 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., Kota-ki 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 vouchers 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; prepodial ovum, prominent; two rounded palmar tubercles; supernumerary tubercles absent; relative length of fingers II < l=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.
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: \(I2–2I1\frac{1}{2}–3III2–3IV3–2\); 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 \(\frac{2}{3}\)rd 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 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.
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., Boa 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 | 92.9904 | 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 | Khudiramapur       | 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 | Khudiramapur       | 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 | Khudiramapur       | 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, Tigapur | 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   | 12.7090      | 92.9680    | 7        |
| 45              | Rangat, Cuthbert Bay | 12.6800      | 92.9400    | 156      |
| 46              | Rangat, Mount Diavalo | 12.6800      | 92.9420    | 98       |
| 47              | Rangat, Dhanni Nallah | 12.6160      | 92.9550    | 11       |
| 48              | Rangat, Moricedera | 12.5535      | 92.9712    | 17       |
| 49              | Rangat, Parangshala | 12.5265      | 92.9053    | 26       |
| 50              | Rangat, Yeratta  | 12.5038      | 92.9028    | 40       |
| 51              | Rangat, Bakultala | 12.5015      | 92.8857    | 119      |
| 52              | Rangat, Shyamkund | 12.4910      | 92.8480    | 38       |
| 53              | Rangat, Sabri    | 12.4861      | 92.9002    | 13       |
| 54              | Rangat, Vishnupur | 12.4840      | 92.8734    | 17       |
| 55              | Rangat, Vishnupur | 12.4756      | 92.8766    | 7        |
| 56              | Rangat, Ullidera | 12.4718      | 92.8613    | 9        |
| 57              | Rangat, Ullidera | 12.4715      | 92.8634    | 10       |
| 58              | Rangat, Bharatpur | 12.4680      | 92.8930    | 16       |
| 59              | Rangat, Bronil   | 12.4631      | 92.8312    | 5        |
| 60              | Rangat, Panchawati | 12.4078      | 92.8877    | 9        |
| 61              | Long Island, Sigman Dera | 12.3820      | 92.9290    | 37       |
| 62              | Long Island, Lalaji Bay Forest | 12.3790    | 92.9350    | 60       |
| 63              | Long Island     | 12.3710      | 92.9220    | 60       |
| 64              | North Passage Island | 12.2880      | 92.9334    | 12       |
| 65              | Baratang Island, Shankar Nallah | 12.2543    | 92.8041    | 64       |
| 66              | Baratang Island, Shankar Nallah | 12.2543    | 92.8041    | 67       |
| 67              | Baratang Island, Loroijgi | 12.2389    | 92.7957    | 37       |
| 68              | Baratang Island, Roglechang | 12.1603    | 92.7936    | 26       |
| 69              | Baratang Island, Baladera | 12.1363    | 92.8069    | 8        |
| 70              | Baratang Island, Baladera | 12.1357    | 92.8032    | 4        |
| 71              | Baratang Island, Jarawa Creek | 12.1250   | 92.7881    | 18       |
| 72              | Baratang Island, Wrafters Creek | 12.1127   | 92.7680    | 45       |
| 73              | Baratang Island, Wrafters Creek | 12.1105   | 92.7725    | 21       |
| 74              | Baratang Island, Wrafters Creek | 12.1066   | 92.7722    | 12       |
| 75              | Baratang Island, Naya Dera | 12.0974    | 92.7515    | 54       |
| 76              | Jirkatang – 21km | 12.0930      | 92.7070    | 73       |
| 77              | Jirkatang Reserve | 12.0581      | 92.7128    | 59       |
| 78              | Jirkatang Reserve, Jirkatang – 16km | 12.0560   | 92.7020    | 89       |
| 79              | Havelock Island, Govind Nagar | 12.0418    | 92.9831    | 6        |
| 80              | Havelock Island, Shyam Nagar | 12.0087    | 92.9635    | 58       |
| 81              | Havelock Island, Krishna Nagar | 12.0076   | 92.9612    | 61       |
| 82              | Jirkatang Reserve, Jirkatang – 6km | 11.9650  | 92.6770    | 105      |
| 83              | Jirkatang       | 11.9455      | 92.6812    | 127      |
| 84              | Jirkatang       | 11.9060      | 92.6660    | 132      |
| 85              | Shoal Bay – 19  | 11.8967      | 92.7662    | 33       |
| 86              | Shoal Bay – 19  | 11.8950      | 92.7650    | 16       |
| 87              | Shoal Bay – 11  | 11.8820      | 92.7470    | 56       |
| 88              | Shoal Bay       | 11.8770      | 92.7410    | 31       |
| 89              | Shoal Bay       | 11.8747      | 92.7402    | 23       |
| 90              | Shoal Bay       | 11.8746      | 92.7406    | 32       |
| 91              | Shoal Bay       | 11.8710      | 92.7420    | 87       |
| 92              | Jirkatang       | 11.8680      | 92.6550    | 82       |
| 93              | Shoal Bay       | 11.8570      | 92.7350    | 21       |
| 94              | Shoal Bay 10    | 11.8438      | 92.7293    | 6        |
| 95              | Shoal Bay 10    | 11.8410      | 92.7290    | 35       |
| 96              | Neil Island     | 11.8354      | 93.0362    | 6        |
| 97              | Shoal Bay – 8   | 11.8270      | 92.7220    | 9        |
| 98              | Kalatang        | 11.8050      | 92.7140    | 27       |
| 99              | Wrightsmayoo Creek | 11.8010   | 92.7080    | 16       |
| 100             | Kalatang        | 11.7958      | 92.7118    | 18       |
| 101             | 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    | 64       |
| 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 | Chidiyatapu                            | 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               | 92.3530    | 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 | Herimdirhar Bay                        | 10.5870               | 92.5330    | 4        |
| 156 Little Andaman | Ongi Tikery                            | 10.5710               | 92.5540    | 34       |

**Minervarya charlesdarwini**

| District / Group | Island / Locality | Coordinates            | Elevation |
|-----------------|-------------------|------------------------|-----------|
| 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) |
| North Andaman   | Kishori Nagar      | 13.2711      | 92.95955   | 62       |
| North Andaman   | Durgapur           | 13.2672      | 93.0382    | 23       |
| North Andaman   | Lamiya Bay         | 13.2037      | 93.0408    | 10       |
| North Andaman   | Khudirampur        | 13.2033      | 92.9691    | 36       |
| North Andaman   | Khudirampur        | 13.2026      | 93.0375    | 72       |
| North Andaman   | Kishori Nagar      | 13.2025      | 92.9690    | 31       |
| North Andaman   | Lamiya Bay         | 13.2010      | 93.0380    | 36       |
| North Andaman   | Saddle Peak        | 13.1967      | 93.0314    | 72       |
| North Andaman   | Lamiya Bay         | 13.1930      | 93.0340    | 54       |
| North Andaman   | Saddle Peak        | 13.1860      | 93.0260    | 54       |
| North Andaman   | Saddle Peak        | 13.1850      | 93.0190    | 219      |
| North Andaman   | Kalara             | 13.1752      | 92.9341    | 47       |
| North Andaman   | Kalpong Dam        | 13.1140      | 92.9971    | 59       |
| North Andaman   | Ram Nagar          | 13.0800      | 93.0151    | 8        |
| North Andaman   | Patti Level        | 13.0596      | 92.9907    | 122      |
| North Andaman   | Interview Island   | 12.8999      | 92.7200    | 22       |
| North Andaman   | Interview Island   | 12.8953      | 92.6884    | 78       |
| Middle Andaman  | Mayabunder, Austin Strait | 12.8934 | 92.8574    | 28       |
| Middle Andaman  | Mayabunder, Tugapur | 12.8395     | 92.8568    | 13       |
| Middle Andaman  | Mayabunder, Hanspuri | 12.7581   | 92.8059    | 73       |
| Middle Andaman  | Mayabunder, Chainpur | 12.7396   | 92.8068    | 28       |
| Middle Andaman  | Rangat, Mount Diavalo | 12.6800  | 92.9420    | 99       |
| Middle Andaman  | Rangat, Moricedera | 12.5535     | 92.9712    | 15       |
| Middle Andaman  | Rangat, Parnashala | 12.5265     | 92.9053    | 24       |
| Middle Andaman  | Rangat, Veratta    | 12.5038     | 92.9028    | 36       |
| Middle Andaman  | Rangat, Bakultala  | 12.5015     | 92.8857    | 119      |
| Middle Andaman  | Rangat, Shyamkund  | 12.4910     | 92.8480    | 36       |
| Middle Andaman  | Rangat, Sabari     | 12.4861     | 92.9002    | 12       |
| Middle Andaman  | Rangat, Vishnupur  | 12.4840     | 92.8734    | 63       |
| Middle Andaman  | Rangat, Ullidera   | 12.4715     | 92.8634    | 15       |
| Middle Andaman  | Rangat, Bharatpur  | 12.4680     | 92.8930    | 16       |
| Middle Andaman  | Rangat, Bronil     | 12.4631     | 92.8312    | 5        |
| Middle Andaman  | Rangat, Panchawati | 12.4078     | 92.8877    | 8        |
| Middle Andaman  | Long Island, Signman Dera | 12.3820 | 92.9290    | 38       |
| Middle Andaman  | Long Island, Lalaji Bay Forest | 12.3790 | 92.9350    | 60       |
| Middle Andaman  | Long Island, Long Island | 12.3710 | 92.9220    | 60       |
| Middle Andaman  | Baratang Island, Shankar Nallah | 12.2543 | 92.8041    | 68       |
| Middle Andaman  | Baratang Island, Shankar Nallah | 12.2543 | 92.8041    | 68       |
| Middle Andaman  | Baratang Island, Lorug | 12.2389   | 92.7957    | 37       |
| Middle Andaman  | Baratang Island, Roglobachang | 12.1603 | 92.7936    | 21       |
| Middle Andaman  | Baratang Island, Baludera | 12.1357 | 92.8032    | 5        |
| Middle Andaman  | Baratang Island, Jarawa Creek | 12.1250 | 92.7881    | 17       |
| Middle Andaman  | Baratang Island, Wrafters Creek | 12.1127 | 92.7680    | 46       |
| Middle Andaman  | Baratang Island, Wrafters Creek | 12.1105 | 92.7725    | 21       |
| Middle Andaman  | Baratang Island, Naya Dera | 12.0974 | 92.7535    | 54       |
| South Andaman   | Jirkatang – 21km   | 12.0930     | 92.7070    | 73       |
| South Andaman   | Jirkatang – 16km   | 12.0560     | 92.7020    | 85       |
| South Andaman   | Jirkatang – 6km    | 11.9650     | 92.6770    | 106      |
| South Andaman   | Jirkatang          | 11.9455     | 92.6812    | 126      |
| South Andaman   | Jirkatang          | 11.9060     | 92.6660    | 133      |
| South Andaman   | Shoal Bay – 19     | 11.8950     | 92.7650    | 16       |
| South Andaman   | Shoal Bay – 19     | 11.8910     | 92.7790    | 13       |
| South Andaman   | Shoal Bay – 1      | 11.8820     | 92.7470    | 57       |
| South Andaman   | Shoal Bay          | 11.8770     | 92.7410    | 29       |
| South Andaman   | Shoal Bay          | 11.8747     | 92.7402    | 25       |
| South Andaman   | Shoal Bay          | 11.8746     | 92.7406    | 55       |
| South Andaman   | Shoal Bay          | 11.8746     | 92.7406    | 55       |
| 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 Shooli Bay              | 11.8570               | 92.7350    | 21       |
| 219              | South Andaman Shooli Bay – 10         | 11.8410               | 92.7290    | 37       |
| 220              | South Andaman Neil Island             | 11.8354               | 93.0362    | 6        |
| 221              | South Andaman Shooli Bay – 8          | 11.8270               | 92.7220    | 9        |
| 222              | South Andaman Kalatang                | 11.8050               | 92.7140    | 23       |
| 223              | South Andaman Wrightmyayo 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 Chidiyatapu             | 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     | 10.7040               | 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 Nallah         | 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**

| District / Group | Island / Locality                     | Coordinates          |
|------------------|---------------------------------------|----------------------|
| 259              | Nicobar, Central group Bompoka Island | 8.2494               |
| 260              | Nicobar, Central group Kamorta Island, | 8.1731               |
| 261              | Kamaka                            | 93.5070              |
| 262              | Nicobar, Central group Kamorta Island, | 8.1198               |
| 263              | Vikas Nagar                       | 93.5138              |
| 264              | Nicobar, Central group Kamorta Island, | 8.0212               |
| 265              | Champin                           | 93.4916              |
| 266              | Nicobar, Central group Nancowry Island, | 8.0202               |
| 267              | Munak                             | 93.5548              |
| 268              | Nicobar, Central group Nancowry Island, | 8.0123               |
| 269              | Kapanga                           | 93.5045              |
| 270              | Nicobar, Central group Katchal Island, | 8.0057               |
| 271              | Malacca                           | 93.4932              |
| 272              | Nicobar, Central group Katchal Island, | 8.0053               |
| 273              | Beachdiera                        | 93.5675              |
| 274              | Nicobar, Central group Katchal Island, | 7.9992               |
| 275              | Kapanga                           | 93.3928              |
| 276              | Nicobar, Central group Katchal Island, | 7.9969               |
| 277              | Kapanga                           | 93.3585              |
| 278              | Nicobar, Central group Katchal Island, | 7.9961               |
| 279              | Beachdiera                        | 93.5315              |
| 280              | Nicobar, Central group Katchal Island, | 7.9879               |
| 281              | Lal Munak                         | 93.3737              |
| 282              | Nicobar, Central group Katchal Island, | 7.9407               |
| 283              | Upper Katchal                     | 93.4434              |
| 284              | Nicobar, Southern group Little Nicobar Island, | 7.4069               |
| 285              | Makachua                          | 93.7096              |
| 286              | Nicobar, Southern group Little Nicobar Island, | 7.3760               |
| 287              | Pulo Panja                        | 93.7395              |
| District / Group | Island / Locality | Coordinates | Elevation (meters) |
|-----------------|-------------------|-------------|-------------------|
|                 |                   | Latitude (°N) | Longitude (°E)    |
| 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, Indira Point | 6.9814 | 93.8642 | 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, Gandha 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, Sastr Subway | 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  |
| 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 | 93.0409 | 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, Veratta | 12.5038 | 92.9028 | 41  |
| 310             | Middle Andaman     | Rangat, Shyamkund | 12.4910 | 92.8480 | 36  |
| 311             | Middle Andaman     | Rangat, Saba | 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    | 11.8750 | 92.7350 | 21  |
| 330             | South Andaman      | Shoal Bay –10 | 11.8410 | 92.7290 | 37  |
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 nominate 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 redescriptions 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
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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.

tvs. 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 ⅔th 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 Boulenger, 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 vouched record of Rana macodon 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 vouched 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 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 minervarian 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 “1¼ th 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.
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-
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 nicobariensis* 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 nearly 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, Uttar Pradesh, 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; Ragasamy 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 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 extensive-
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 distributions, 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 Vasurevan 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 chakrapani*, *M. nakkavaram* (Garg et al. 2019, 2022), *Fejervarya limnocharis*, *F. moodiei* (Chandramouli et al. 2020b), *Bijuana 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 erythrea*) 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 minervayan 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. mysoresensis* 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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