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## Systematic revision of *Microhyla* (Microhylidae) frogs of South Asia: a molecular, morphological, and acoustic assessment

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## Abstract

This study presents a systematic revision of South Asian members of the taxonomically challenging genus *Microhyla* Tschudi, 1838. Species relationships and diagnostic characters are determined by integrating molecular, morphological, and acoustic approaches, through which we also recognize six groups of closely related species. In addition, a new species from the southern Western Ghats of India is formally described as *Microhyla darreli* **sp. nov.** Species accounts of all the 16 recognized members from South Asia include current taxonomic status, metric and meristic characters, divergence in mitochondrial DNA, phylogenetic relationships, acoustic characters, revised geographical distributions, and natural history notes. Molecular and morphological relationships of three poorly known members *— M. chakrapanii, M. karunaratnei*, and *M. zeylanica* — are clarified for the first time since their original descriptions. The presence of *M. berdmorei* and another potential new species close to *M. heymonsi* in India is genetically confirmed, and several misidentifications are corrected. For comparative purposes, molecular, morphological, and acoustic relationships are also discussed for eight closely related East and Southeast Asian species. Consequently, insights from this study will facilitate a much-needed comprehensive revision of the Pan-Asian frog genus *Microhyla*.

## Key words

Amphibians; bioacoustics; cryptic species; diagnostic characters; integrative taxonomy; Microhylidae; molecular phylogeny; morphology; species groups; new species.

## Introduction

The genus *Microhyla* Tschudi, 1838 (family Microhylidae) currently comprises of 42 small to medium-sized (SVL 10-46 mm), narrow-mouthed, and ground-dwelling frogs that are widely distributed in South, Southeast, and East Asia. It is also the most speciose (AMPHIBIAWEB, 2018; FROST, 2018) and wide-ranging genus of the Asian

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subfamily Microhylinae (MATSUI et al., 2011). Species in this genus usually occupy habitats ranging from natural forests to human-altered landscapes. Despite common occurrence, genus Microhyla has remained one of the most challenging taxonomical group of microhylid frogs, mainly because of the small size, conserved morphology, and wide distribution of its members across Asia (e.g., MATSUI et al., 2005, 2011). In recent years, the use of molecular data has significantly aided delineation of known taxa (e.g., MATSUI et al., 2005, 2011; MAT-SUI, 2011; HASAN et al., 2012; YUAN et al., 2016; GARG et al., 2018A) and identification of new cryptic species (MATSUI, 2011; MATSUI et al., 2013; HASAN et al., 2014A; HOWLADER et al., 2015; WIJAYATHILAKA et al., 2016; SE-SHADRI et al., 2016A; KHATIWADA et al., 2017), leading to a continuous increase in the number of recognized Microhyla species. However, lack of molecular information for several known species (at least 13 species), continues to deter a thorough taxonomic revision of this group. The latest available systematic study addressing species from the entire known range of the genus provided significant insights on phylogenetic relationships among Microhyla frogs (MATSUI et al., 2011); however, the South Asian members remained poorly represented, i.e., only two out of six formerly known regional endemics (from the countries of Bangladesh, Bhutan, India, Nepal, Pakistan, and Sri Lanka). Furthermore, subsequent research has doubled the number of Microhyla species occurring in South Asia (HASAN et al., 2014A; HOWLADER et al., 2015; WIJA-YATHILAKA et al., 2016; SESHADRI et al., 2016a; KHATIWADA et al., 2017; VINEETH et al., 2018), consequently elevating the prominence of this region for Microhyla diversity.

The taxonomy of South Asian Microhyla has also been in a state of flux. Until recently, long-standing confusions concerning identification and range delineation existed for many species, including some of the oldest known members such as Microhyla ornata (Duméril & Bibron, 1841), M. rubra (Jerdon, 1854 "1853"), and M. sholigari Dutta & Ray, 2000 (MATSUI et al., 2005; WIJAYATHILAKA et al., 2016; SESHADRI et al., 2016B; GARG et al., 2018A). The systematic relationships of three other species — M. chakrapanii Pillai, 1977, M. karunaratnei Fernando & Siriwardhane, 1996, and M. zeylanica Parker & Osman-Hill, 1949 — are still unknown. Moreover, recent species descriptions largely include literaturebased comparisons with closely related congeners (e.g., HASAN et al., 2014A; SESHADRI et al., 2016A; VINEETH et al., 2018), lacking attempts to study available types, museum specimens, or new collections from original type localities. Hence altogether, the South Asian Microhyla frogs remain poorly understood.

In this work, we study all the known *Microhyla* species of South Asia based on an integrated molecular, morphological, and acoustic assessment; this utilized newly obtained primary data from field work, and study of available types and additional museum specimens. Our study also uncovers a new *Microhyla* species from India, provides insights on poorly known taxa, presents new distribution records, and recognizes species groups accommodating all South Asian members. Additionally, relationships with close congeners from Southeast and East Asia are discussed based on comparative material from outside the range to facilitate systematic conclusions.

## Materials and methods

#### Field surveys and data collection

Frogs were sampled during field surveys conducted between 2002-2017 at over 90 localities across India and Sri Lanka in South Asia, and Indonesia in Southeast Asia. Detailed list of species and localities surveyed in the present study along with taxa incorporated from previous studies are provided in Table S1. Adult specimens and larvae were mostly sampled during the breeding season, from May to September; random opportunistic searches were also conducted outside this period. Adult males were often located by their advertisement calls. Calls were recorded using a Marantz PMD620 or Fostex FR2LE solid-state digital recorder (44.1 kHz sampling rate, 16-bit resolution) with Sennheiser ME66 or MKH 416 unidirectional microphone. One specimen from each of the recorded populations was collected for morphological and genetic identification. Sampled individuals were photographed, followed by euthanisation in Tricaine methanesulphonate (MS-222) solution, fixation in 4% formalin, and preservation in 70% ethanol. Tissue samples for molecular studies were obtained from the thigh (adult) or tail (tadpole) muscle and preserved in absolute ethanol. Geographical coordinates were recorded using a Garmin 76CSx GPS with the WGS84 datum system. Distribution maps were prepared in QGIS version 2.6.1 (http://www.qgis.org). Type specimens from the present study are deposited in the Zoological Survey of India -Western Ghats Regional Centre (ZSI-WGRC), Calicut, India.

#### Molecular study

Extraction of genomic DNA from 48 tissue samples was carried out using DNeasy blood and tissue kit (Qiagen, Valencia, CA, USA), following the manufacturer's protocol. For all the samples, a fragment of ca. 540 bp of the mitochondrial (mt) 16S ribosomal RNA gene (16S) was PCR-amplified using standard protocols and the primer set 16Sar and 16Sbr previously published by SIMON *et al.* (1994). Additionally, a fragment of ca. 700 bp of the nuclear (nu) brain derived neurotrophic factor gene (BDNF) was amplified using the primer set BDNF.Amp. F1 and BDNF.Amp.R1 (VAN DER MEIJDEN *et al.*, 2007) for selected taxa representing all known and newly recognized South Asian *Microhyla* species (Table S1). Sequencing was performed on both strands using BigDye

Terminator v3.1 Cycle Sequencing Kit on ABI 3730 automated DNA sequencer (Applied Biosystems). Sequences were assembled and checked in ChromasPro v1.34 (Technelysium Pty Ltd.). GenBank accession numbers for sequences generated as part of this study are MH807384–MH807439 (Table S1).

The newly generated 16S sequences were first assembled in MEGA 6.0 (TAMURA et al., 2013) along with all previously available homologous sequences for Microhyla species from GenBank. A dataset of 539 bp using a total of 347 Microhyla sequences and an additional outgroup taxon Kaloula pulchra (VAN BOCXLAER et al., 2006), was aligned using ClustalW in MEGA and subjected to Neighbor-Joining (NJ) analysis in PAUP\* (Swofford 2002). Based on preliminary clustering of samples in the NJ tree, one exemplar representing each Microhyla species was selected either from the type series, topotypes, or populations nearest to the type localities. A concatenated dataset comprising 1,230 bp of the mitochondrial 16S (528 bp, excluding ambiguously aligned regions) and nuclear BDNF (702 bp) genes from 35 Microhyla species and the outgroup taxon was assembled for further phylogenetic analyses. For the Maximum Likelihood (ML) analysis, heuristic searches were performed in PAUP\* (Swofford 2002) using the GTR+I+G model of DNA evolution that was determined by implementing Akaike Information Criterion in ModelTest 3.5 (POSADA & CRANDALL, 1998). Clade support was assessed both with 10,000 rapid bootstrap replicates (GTRGAMMA model) executed using RAxML 7.3.0 (STAMATAKIS et al., 2008) in raxmlGUI 1.1 (SILVESTRO & MICHALAK, 2012), and Bayesian Posterior Probabilities inferred using Mr-Bayes 3.1.2 (RONQUIST & HUELSENBECK, 2003). For the Bayesian analysis, two parallel runs of four Markov Chain Monte Carlo (MCMC) chains were executed for 10 million generations using the GTR+I+G model. Trees were sampled once per 1,000 generations and summarized after discarding the first 25 percent as burn-in. Convergence was determined by average standard deviation of the split frequencies of < 0.01 and potential scale reduction factors of  $\sim$  1.0, and stationarity of the runs was observed through the log likelihood trends. Further, the available BDNF gene sequences (Table S1) were used for constructing a Median-Joining haplotype network in the software Network 4.6.1.0 (www.fluxus-engineering. com) using phased data generated after performing the PHASE algorithm (STEPHENS et al., 2001) in DnaSP version 5 (LIBRADO & ROZAS, 2009).

Based on phylogenetic relationships in the concatenated mt + nu DNA ML tree, and evidence from our morphological and acoustic studies (see the relevant result sections), group-wise ML trees were constructed with all available 16S sequences using PAUP\* (SwoFFORD, 2002). Clade support was assessed with rapid RAxML bootstrap replicates and Bayesian analysis, as dicussed above. Intra- and interspecific uncorrected pairwise distances for 16S (using all sites) were also computed using PAUP\* (SwoFFORD, 2002), for all individuals in each of the species groups.

#### Morphological study

Adult specimens were morphologically examined using a stereomicroscope to study the metric and meristic characters. Sex and maturity were determined either by the presence of vocal sacs in males or by examining the gonads through a ventral incision. The following measurements were taken using digital slide-calipers and noted to the nearest 0.1 mm: SVL (snout-vent length), HW (head width, at the angle of the jaws), HL (head length, from the rear of the mandible to the tip of the snout), SL (snout length, from the tip of the snout to the anterior orbital border), EL (eye length, horizontal distance between the bony orbital borders), EN (distance from the front of the eye to the nostril), NS (distance from the nostril to the tip of the snout), IN (internarial distance), IUE (inter upper eyelid width, shortest distance between the upper eyelids), UEW (maximum upper eyelid width), IFE (internal front of the eyes, shortest distance between the anterior orbital borders), IBE (internal back of the eyes, shortest distance between the posterior orbital borders), FAL (forearm length, from the flexed elbow to the base of the outer palmar tubercle), HAL (hand length, from the base of the outer palmar tubercle to the tip of the third finger), THL (thigh length, from vent to the knee), SHL (shank length, from knee to the heel), FOL (foot length, from the base of the inner metatarsal tubercle to the tip of the fourth toe), TFOL (distance from the heel to the tip of the fourth toe), FD (maximum disc width of finger), FW (width of finger, measured at the base of the disc), TD (maximum disc width of toe), TW (width of toe, measured at the base of the disc), OMTL (length of outer metatarsal tubercle), IMTL (length of inner metatarsal tubercle), FL (finger length, from tip of the digit to its base where it joins the adjacent digit). Digit number is represented by roman numerals I-V in subscript. Measurements and associated terminologies follow BIJU et al. (2014A) and GARG et al. (2018B). All morphometric measurements discussed in the text are in millimeters.

The studied Microhyla species were categorized as: small (male SVL 13-20 mm), medium (male SVL 21-30 mm), and large (male SVL > 31 mm). The webbing formulae follow SAVAGE & HEYER (1967) as modified by Myers & DUELLMAN (1982), and the degree of webbing is described by numbering the subarticular tubercles 1-3, starting from the toe discs (BIJU *et al.*, 2014B); webbing was categorized as rudimentary (slightly above the basal subarticular tubercles on all toes); small (webbing on toe IV beyond the third subarticular tubercle but below the second subarticular tubercle on either side), medium (webbing on toe IV beyond the second subarticular tubercle but below the first subarticular tubercle on either side), and large (webbing on toe IV extending beyond the first subarticular tubercle on either side), following GARG & BIJU (2017). The following characters are common to all South Asian Microhyla species and consequently not repeated in the descriptions: externally indistinct tympanum, absence of vomerine teeth, absence of webbing between fingers, and single vocal sac in males.

The internal morphology of toes was examined under a stereomicroscope using maceration and clearing procedures (TAYLOR & VAN DYKE, 1985) without staining. Terminologies used to describe the shape of terminal phalanges (simple, knobbed, T-shaped, and Y-shaped) follow PARKER (1927) and LYNCH (1971). Photographs and drawings were made with the aid of camera lucida or Nikon's Digital Sight DS-U3 camera mounted on SMZ 1500 stereomicroscope.

In order to assess the degree of morphometric differentiation among *Microhyla* species, Principal Component Analysis (PCA) was performed in the software Statistica v7.1 (StatSoftInc) using standardized morphometric data from adult male specimens. Principal Components (PC) with eigenvalues > 1.0 were used to understand morphological variations, and factor scores from the first two components were further observed on scatterplots.

The following institutional abbreviations are used: AMS (Australian Museum, Sydney, Australia), NMSL (National Museum of Sri Lanka, Colombo, Sri Lanka), ANSP (Academy of Natural Sciences of Philadelphia, USA), BMNH (British Museum of Natural History, London, United Kingdom), BNHS (Bombay Natural History Society, Bombay, India), CIB (Chengdu Institute of Biology, Chengdu, China), DZ (Department of Molecular Biology & Biotechnology, University of Peradeniya, Sri Lanka), IABHU (Institute for Amphibian Biology, Hiroshima University, Japan), MNHNP (Museum National d'Histoire Naturelle, Paris, France), MZH (Finnish Museum of Natural History, Finland), NCBS (National Centre for Biological Sciences, Bangalore, India), NHM (Natural History Museum, London, United Kingdom), SDBDU (Systematics Lab, University of Delhi, India), UIMZ (Museum of Zoology, Research Center for Climate Change, University of Indonesia), WII (Wildlife Institute of India, Dehradun, India), ZMB (Zoologisches Museum, Berlin, Germany), ZSIC (Zoological Survey of India, Kolkata, India), ZSI-SRS (Zoological Survey of India-Southern Regional Station, Chennai, India), ZSI-WGRC (Zoological Survey of India-Western Ghats Regional Centre, Calicut, India).

#### Acoustic study

Acoustic properties for five calls of each species were measured using Raven Pro 1.4 (CHARIF *et al.*, 2010). Five temporal properties (call duration, call rise time, call fall time, number of pulses per call, and pulse rate) and one spectral property (overall dominant frequency) were used for analyses. Oscillograms and spectrograms were prepared for graphical representation of the call. Call property definitions and associated terminologies follow BEE *et al.* (2013); studied calls were categorized, based on average call duration, as short pulsatile (< 200 ms), medium pulsatile (200–500 ms), and long pulsatile (> 500 ms). Call recordings are available in the supplemental material.

#### Author contributions

SDB and SG conceived and designed the study; SDB secured funding for the study; MM secured funding for research in Sri Lanka; SDB, SG, RS, AD, NAA, KKV (India), MM, NW, GS (Sri Lanka), FA, AATA (Indonesia), and JPJ (China), collected material and/or generated data; SG, SDB, and RS analyzed the data; SG and SDB wrote the manuscript; all authors reviewed and edited the manuscript drafts.

### Results

Our study confirms the presence of total 16 *Microhyla* species in South Asia; 14 previously known species (*M. berdmorei*, *M. chakrapanii*, *M. karunaratnei*, *M. kodial*, *M. laterite*, *M. mihintalei*, *M. mukhlesuri*, *M. mymensinghensis*, *M. nilphamariensis*, *M. ornata*, *M. rubra*, *M. sholigari*, *M. taraiensis*, and *M. zeylanica*), one tentatively identified taxon (*M. cf. heymonsi*), and an additional new species. The presence of *M. butleri* and *M. heymonsi* in South Asia is considered doubtful, as their previous reports are shown to be misidentifications (see notes under the species accounts of *M. berdmorei*, *M. cf. heymonsi*, and *M. mymensinghensis*). Systematic relationships among South Asian *Microhyla* species and their close congeners from East and Southeast Asia are presented in the below sections.

#### Phylogenetic relationships

The relationships recovered in our mt + nu phylogenetic tree (Fig. 1) were largely in agreement with previous studies based on mt DNA (e.g., MATSUI et al., 2005, 2011; MATSUI, 2011; HASAN et al., 2012; MATSUI et al., 2013; HOWLADER et al., 2015; WIJAYATHILAKA et al., 2016; SE-SHADRI et al., 2016B; YUAN et al., 2016; KHATIWADA et al., 2017). As shown previously (MATSUI et al., 2011; PELOSO et al., 2016), the genetically represented Asian Microhyla species were divided into two geographical subgroups: Southeast Asian (SEA, clade B), with five known species — M. annectens, M. marmorata, M. nanapollexa, M. perparva, and M. petrigena; and Pan-Asian (PA, clade A), including all other South, Southeast, and East Asian members (Fig. 1). Our study focuses on relationships among members of the latter group since it includes all the 16 recognized South Asian species, i.e., 14 previously known and two additional unidentified lineages. Among the known taxa, molecular data is presented for the first time for three poorly known species — M. chakrapanii, M. karunaratnei, and M. zeylanica. The following six major clades comprising of South Asian members and close relatives from East and Southeast Asia were recovered: (1) Microhyla achatina group: M. achatina, M. borneensis, M. heymonsi, M. cf. heymonsi, M. kodial, *M. malang, M. mantheyi*, and *M. orientalis*; (2) *Microhyla berdmorei* group: *M. berdmorei* and *M. pulchra*; (3) *Microhyla fissipes* group: *M. chakrapanii, M. fissipes, M. mixtura, M. mukhlesuri, M. mymensinghensis*, and *M. okinavensis*; (4) *Microhyla ornata* group: *M. nilphamariensis, M. ornata*, and *M. taraiensis*; (5) *Microhyla rubra* group: *M. mihintalei* and *M. rubra*; and (6) *Microhyla zeylanica* group: *M. karunaratnei, M. laterite*, *M. sholigari, M. zeylanica*, and one potential new species, subsequently described as *Microhyla darreli* **sp. nov.** (see below). Apart from these, three species (*M. butleri, M. palmipes*, and *M. superciliaris*) could not be confidently assigned to any of the groups, however their phylogenetic positions were in agreement with previous studies (e.g., MATSUI et al., 2011).

Species-level relationships were further investigated based on group-wise phylogenetic analyses using multiple 16S gene sequences, which were available for all the *Microhyla* species included in this study. Inter- and intraspecific differentiation was also assessed on the basis of genetic distances in the mitochondrial 16S gene (Table S2). The relationships observed in species group trees were largely in consensus with Fig. 1, with a few exceptions (see 'genetic relationships' under each group).

In the nuclear gene haplotype network, none of the included Microhyla species (except M. darreli sp. nov. and M. laterite) showed sharing of haplotypes, and the species clusters were largely congruent with the phylogenetically and morphologically recognized groups (Fig. 2). All species groups were separated by at least six mutational steps, with the exception of M. berdmorei and *M. heymonsi* that were separated only by three steps. The Microhyla achatina group was poorly delineated probably due to missing data for several known members from regions outside South Asia. Another species, M. okinavensis, was placed distantly from the Microhyla fissipes group with a minimum of 16 mutational steps. Close genetic relationships were also observed among species from geographically distant regions across South, Southeast, and East Asia, suggesting complex patterns of diversification among the Microhyla frogs of Asia.

#### Morphometric differentiation

Morphometric differentiation was assessed based on Prinicpal Component Analysis (PCA) using 40 characters from 120 specimens representing 14 South Asian *Microhyla* species and six closely related congeners from Southeast and East Asia. The PCA factor loadings representing the composition of each PCA factor are shown in Table S3. The first four PCA factors with eigenvalues more than 1.0 explained 82.4% of the total variance observed among these species. PCA factor 1 was correlated with most of the morphological parameters (36 out of 40 variables) and explained 66.8% of the variance (Table S3). On the other hand, OMTL was the only significantly correlated morphological variable with PCA factor 2, accounting for 8.8% of the variance. The remaining PCA factors explained an additional 24.4% of the variance. The projection of species on factor planes 1 and 2 (Fig. 3) showed considerable overlaps among species as well as the species groups. Five species, M. berdmorei, M. pulchra, M. mihintalei, M. rubra, and *M. kodial* formed relatively distinct clusters, whereas, members of Microhyla fissipes group, Microhyla ornata group, Microhyla zeylanica group, and to certain extent Microhyla achatina group, failed to separate out on the factor planes. At the group-level, relatively better morphological differentiation was observed; Microhyla rubra group (M. mihintalei and M. rubra) and Microhyla berdmorei group (M. berdmorei and M. pulchra) formed the most distinct clusters. Although members of Microhyla fissipes group, Microhyla ornata group, and Microhyla zeylanica group clustered respectively in the morphospace, the groups themselves were not clearly separated. For example, members of Microhyla fissipes group (M. mukhlesuri and M. mymensinghensis) overlapped with Microhyla achatina group (M. achatina and M. heymonsi). On the other hand, the relatively smallersized members of Microhyla achatina group (M orientalis and M. kodial) showed considerable resemblance with Microhyla zeylanica group (M. darreli sp. nov., M. karunaratnei, M. laterite, M. sholigari, and M. zeylanica). Similarly, members of Microhyla fissipes group (M. fissipes, M. mixtura, and M. mymensinghensis) and Microhyla ornata group (M. nilphamariensis and M. ornata) also showed considerable morphometric resemblance. Altogether, the morphometric data alone was not found very useful to understand the morphological differentiation among the various Microhyla species. Based on these results, we therefore identified a set of meristic characters to understand intra and interspecific variations (Figs. S1, S2), and used a combination of both metric and meristic characters for diagnosis of species and species groups in this morphologically cryptic genus of microhylid frogs.

#### Taxonomic grouping of species

Taxonomic grouping of species within the genus Microhyla based on morphological traits (PARKER, 1934), as previously discussed by DUBOIS (1987), would accommodate the South Asian members in two groups: Microhyla berdmorei group (11 species) and Microhyla achatina group (five species). However, subsequent phylogenetic studies had proposed four groups - Microhyla palmipes group, Microhyla ornata group, Microhyla butleri group, and Microhyla achatina group (MATSUI et al., 2011), and another subgroup, Microhyla borneensis group, was added to accommodate M. orientalis, M. borneensis, M. mantheyi, and M. malang (MATSUI et al., 2013). This grouping was based on phylogenetic relationships (MATsui et al., 2011; MATSUI et al., 2013). Herein, we propose a revised scheme for grouping of the South Asian Microhyla species, based on both morphological and phylogenetic evidence: (1) Microhyla achatina group (M. kodial); (2) Microhyla berdmorei group (M. berdmorei); (3) Microhyla fissipes group (M. chakrapanii, M. mukhlesuri, and M. mymensinghensis); (4) Microhyla ornata group (M. nilphamariensis, M. ornata, and M. taraiensis); (5) Microhyla rubra group (M. mihintalei and M. rubra); and (6) Microhyla zeylanica group (M. darreli **sp. nov.**, M. karunaratnei, M. laterite, M. sholigari, and M. zeylanica). In addition, M. cf. heymonsi (from Andaman Islands, India) is provisionally assigned to the Microhyla achatina group.

## Systematic accounts

#### Microhyla achatina species group

(Figures 1-9, S1, S2; Tables S1-S5; Files S1, S2)

**Members included.** South Asia — *Microhyla kodial* and *provisionally M.* cf. *heymonsi*; Southeast Asia — *M. achatina, M. borneensis, M. malang, M. mantheyi, M. orientalis*, and provisionally *M. heymonsi*.

Diagnosis. The group is distinguished from other Microhyla groups of South Asia by the following suite of morphological characters: small to medium-sized adults (male SVL 14-22 mm; female SVL 22-23 mm); nostrils placed towards the lateral sides of the snout; small finger discs with or without dorso-terminal grooves, cover bifurcate distally; small toe discs with prominent dorso-terminal grooves, cover bifurcate distally; terminal phalanges of toes T-shaped; inner metatarsal tubercle distinct, elongate; outer metatarsal tubercle small, rounded; webbing between toes rudimentary (M. achatina, M. kodial, and M. orientalis); dorsal skin shagreened to prominently granular; a narrow mid-dorsal skin fold or line extending from tip of the snout to the vent (except M. kodial); a prominent streak (white or light brown in life, and grey in preservation) extending from posterior corner of the eye to the shoulder (Fig. 4).

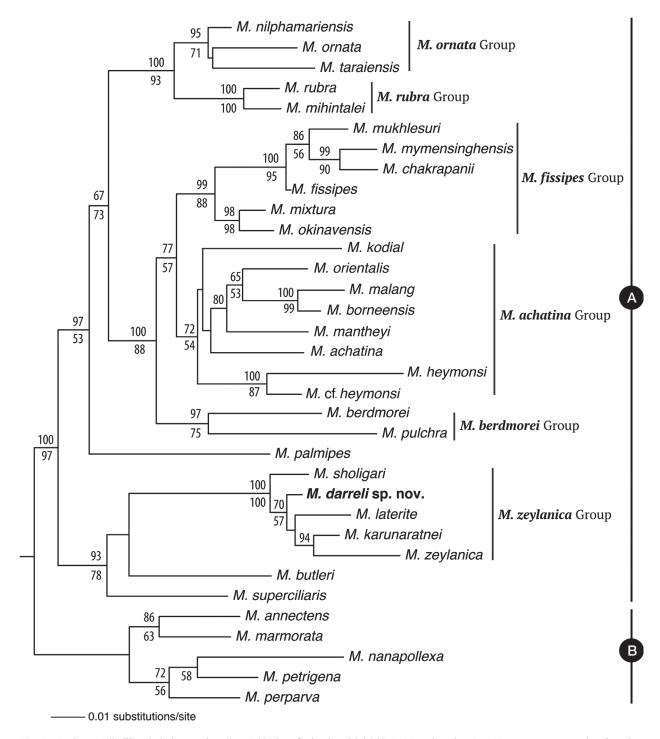
Morphological comparison. Species in this group differ from members of Microhyla berdmorei group by relatively smaller adult size, male SVL 14-22 mm, female SVL 22-23 mm (vs. relatively larger, male SVL 33-36 mm), and rudimentary or small foot webbing, not extending beyond the third subarticular tubercle on either side of toe IV (vs. large, extending beyond the first subarticular tubercle); from Microhyla fissipes group by toe discs with prominent dorso-terminal grooves and cover bifurcate distally (vs. without grooves), and a prominent streak (white or light brown in life, and grey in preservation) extending from posterior corner of the eye to the shoulder (vs. faint); from Microhyla zeylanica group by nostrils placed on lateral side of the snout (vs. more towards the dorsal side); from Microhyla ornata group by toe discs with prominent dorso-terminal grooves and cover bifurcate distally (vs. without grooves); from Micro*hyla rubra* group by relatively smaller adult size, male SVL 14–22 mm, female SVL 22–23 mm (vs. relatively larger, male SVL 21–30 mm, female SVL 23–31 mm), toe discs with prominent dorso-terminal grooves and cover bifurcate distally (vs. rounded without discs and grooves), terminal phalanges of toes T-shaped (vs. simple with rounded tips), and relatively weak elongate inner and rounded outer metatarsal tubercles (vs. well-developed shovel-shaped inner and outer metatarsal tubercles).

**Genetic relationships.** Phylogenetically, *Microhyla achatina* group can be characterized as the most inclusive clade that contains *M. achatina*, *M. borneensis*, *M. kodial*, *M. malang*, *M. mantheyi*, *M. orientalis*, and two undescribed lineages — *M.* "sp. 1" and *M.* "sp. 3" (MATSUI *et al.*, 2011), but none of the other clades that have been genetically studied so far within the entire radiation of *Microhyla*. In this group, we provisionally also include the *Microhyla* '*heymonsi*' clade (*M. heymonsi* + *M.* cf. *heymonsi*) due to close genetic relationship, although its phylogenetic relationship with other members remains poorly resolved (Figs. 1, 4).

The relationships among five Southeast Asian species of this group (Figs. 1, 4) were as previously reported (MATSUI et al., 2011, 2013). The recently described South Asian M. kodial was basal to all other members, albeit with weak support (Figs. 1, 4). In the group-wise mt analysis, the undescribed M. "sp. 3" showed sister relationship with M. achatina (MATSUI et al., 2011), however the position of *M*. "sp. 1" remained unresolved (Fig. 4). The Microhyla 'heymonsi' clade (Microhyla heymonsi + M. cf. heymonsi) formed a weakly supported sister relationship with all other known members of the group in the mt + nu analysis (Fig. 1), however, in the group-wise mt analysis with multiple samples, it was embedded within the Microhyla achatina group (not shown). For detailed discussion on intra- and interspecific pairwise divergence see the respective 'species' accounts and Table S2.

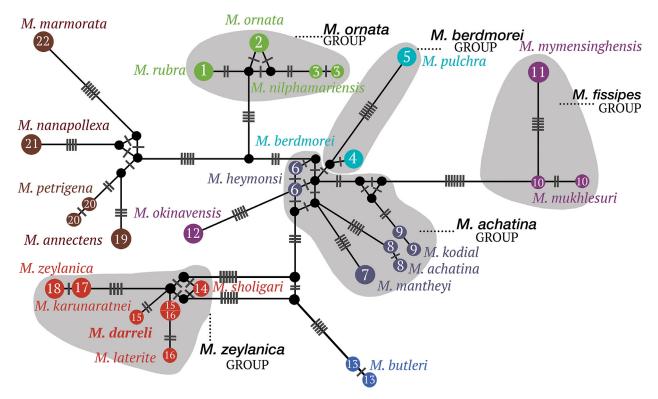
Within the Microhyla 'heymonsi' clade six divergent lineages were recovered with high interspecific genetic distances, congruent with previous work in suggesting that *M. 'heymonsi*' is a complex of multiple species (SHERIDAN, BICKFORD & SU, 2010). A South Asian Microhyla population from Andaman Islands (India) was closely related to M. heymonsi, hence referred to as M. cf. heymonsi (Figs. 1, 8). This population was genetically most close to populations from the neighboring countries of Malaysia and Singapore (sub-clade 1), albeit with considerable divergence of 2.1-2.7%. It was also found to have high genetic divergence of 4.2-6.2% with the clade constituting typical Chinese populations (sub-clade 4), while the divergence between entire sub-clade 1 and sub-clade 4 ranged from 4.2–6.4%. For detailed pairwise comparison among populations comprising the Microhyla 'heymonsi' clade and sub-clades 1-6, see Table S2.

Acoustic comparison. Species in this group can be differentiated from the other groups by their medium-sized pulsatile calls, 220–290 ms. The overall call structure



**Fig. 1.** Maximum Likelihood phylogram based on 1,230 bp of mitochondrial 16S rRNA and nuclear BDNF gene sequences, showing phylogenetic relationships among all the known South Asian *Microhyla* species (clade A) and congeners from Southeast and East Asia (clades A & B). Six species groups recognized in the study are indicated with vertical lines across the included members. Bayesian Posterior Probabilities (BPP) and RAxML bootstrap values of > 50% are indicated above and below the branches, respectively.

of this group is relatively distinct, but it has close resemblance with *Microhyla ornata* group, from which it differs by shorter call durations, 220-290 ms (vs. longer, 320-340 ms), and higher dominant frequency, 3.3-3.8 kHz (vs. lower, 2.3-3.3 kHz) (Fig. 6; Table S4). Since the calls of *M. orientalis* were considerably different from other studied members of the group (*M. achatina* and *M. kodial*) they are excluded from comparisons. Interestingly, our study found *Microhyla orientalis* to be morphologically close to *M. achatina* and *M. kodial*, however the call of *M. orientalis* is considerably different from the two species. Previously, a separate subgroup was suggested to accommodate this species along with *M. mantheyi*, *M. borneensis*, and *M. malang* (MATSUI *et al.*, 2013). Although, further studies based on robust phylogenies combined with morphological and acoustic evi-



**Fig. 2.** Median-Joining network showing relationships among phased nuclear BDNF gene haplotypes representing 12 *Microhyla* species of South Asia along with congeners from Southeast and East Asia. Circle sizes are proportional to the number of haplotypes, circle colors depict the recognized species groups, circle numbers indicate species, black circles represent median vectors, vertical bars on branches represent the number of mutational steps.

dence could provide more insights on this grouping, we provisionally place *M. kodial* in the *Microhyla achatina* group based on evidence available from our study.

## *Microhyla kodial* Vineeth, Radhakrishna, Godwin, Anwesha, Rajashekhar & Aravind, 2018

Mangaluru Narrow-mouthed Frog (VINEETH et al., 2018)

(Figures 1-4, 6, 7, S1, S2; Tables S1-S5; File S1)

**Original name and description.** *Microhyla kodial* Vineeth K.K., Radhakrishna U.K., Godwin R.D., Anwesha S., Rajashekhar K.P. & Aravind N.A. 2018. A new species of *Microhyla* Tschudi, 1838 (Anura: Microhylidae) from West Coast of India: an integrative taxonomic approach. *Zootaxa* 4420: 151–179. **Type.** Holotype NCBS-AY587, an adult female, by original designation. **Type locality**. "Baikampady, Mangaluru, Dakshina Kannada District, Karnataka, India". **Current status of specific name.** Valid name, as *Microhyla kodial* Vineeth, Radhakrishna, Godwin, Anwesha, Rajashekhar & Aravind, 2018.

**Description of holotype.** A detailed description is available (VINEETH *et al.*, 2018).

**Morphological comparison.** *Microhyla kodial* cannot be confused with any other known *Microhyla* species of South Asia. It differs from all these species by its dorsal

skin shagreened with prominent granular projections (vs. shagreened to sparsely granular, except in some populations of *M. ornata*); absence of mid-dorsal skin fold or line (vs. present); and a faint lateral marking extending from posterior corner of the eye and approaching the groin (vs. prominent and dark lateral band, marking or skin fold starting from tip of the snout or nostril and approaching the groin in all species; interrupted lateral markings or skin fold in *M. berdmorei*).

Microhyla kodial is closely related to the Indonesian species *M. achatina* and *M. orientalis* by its nostrils placed on lateral side of the snout; toe tips with prominent dorso-terminal grooves and cover bifurcate distally; rudimentary webbing between toes; and presence of a lateral streak (white or light brown in life and grey in preservation) or skin fold extending from posterior corner of the eye to the shoulder. However, it differs from these two species in having faint lateral marking that extends from posterior corner of the eye and approaches the groin (vs. prominent and dark lateral band, marking or skin fold starting from tip of the snout or nostril and approaching the groin); absence of mid-dorsal skin fold or line (vs. present, extending from tip of the snout to the vent); and ventral surface of foot uniformly pale grey in preservation without markings (vs. light to dark brown with off-white markings from the tip of toe V to the heel). Specifically, *M. kodial* also differs from *M. achatina* by its smaller snout-vent size, male SVL 14–19 mm, N=7, female SVL 18–20 mm, N=2 (vs. larger, male SVL

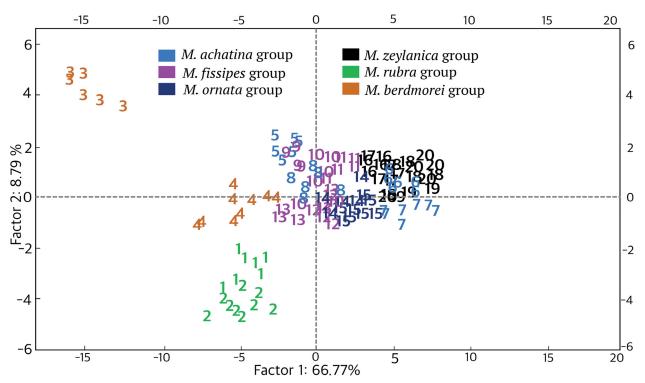


Fig. 3. Principal Component Analysis (PCA) based on 40 morphometric variables depicting the variance observed among 20 species and six recognized species groups in the morphologically cryptic genus *Microhyla*. Total 15 South Asian *Microhyla* species and five closely related congeners from Southeast and East Asia are represented. Species groups are shown in color and each species is indicated by numbers: (1) *M. rubra*, (2) *M. mihintalei*, (3) *M. berdmorei*, (4) *M. pulchra*, (5) *M. achatina*, (6) *M. orientalis*, (7) *M. kodial*, (8) *M. heymonsi*, (9) *M. mukhlesuri*, (10) *M. mymensinghensis*, (11) *M. chakrapanii*, (12) *M. fissipes*, (13) *M. mixtura*, (14) *M. nilphamariensis*, (15) *M. ornata*, (16) *M. zeylanica*, (17) *M. sholigari*, (18) *M. laterite*, (19) *M. karunaratnei*, (20) *M. darreli* sp. nov.

21-23 mm, N=6, female SVL 29 mm, N=1); and dorsal skin shagreened with prominent granular projections (vs. shagreened) (Fig. 7).

Furthermore, *M. kodial* differs from *M. heymonsi* by its dorsal skin shagreened with prominent granular projections (vs. shagreened); absence of mid-dorsal skin fold or line (vs. present, extending from tip of the snout to the vent); faint lateral marking that extends from posterior corner of the eye and approaches the groin (vs. prominent and dark blackish-brown lateral band, marking or skin fold starting from the tip of snout or nostril and approaching the groin); and absence of '()' shaped marking on the mid-dorsum (vs. present).

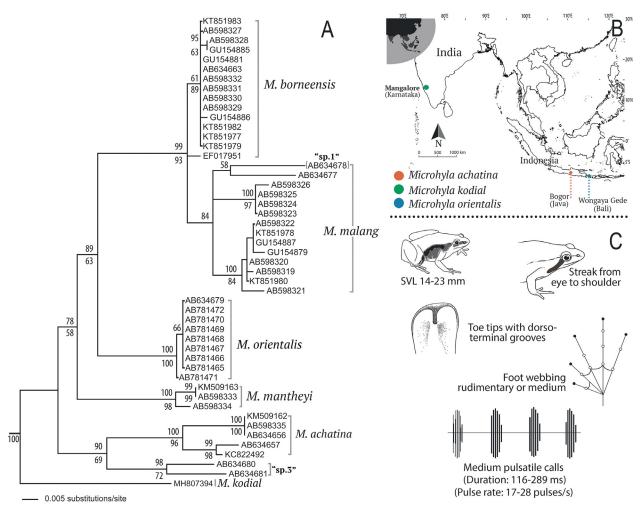
**Genetic comparison.** The average uncorrected sequence divergence between *Microhyla kodial* and all available homologous 16S sequences is  $\geq 6.8\%$ . However, based on phylogenetic as well as morphological evidence, *M. kodial* is closely related to members of the *Microhyla achatina* group and differs from them by the following genetic distances: *M. achatina* (7.4–8.3%), *M. borneensis* (6.8–7.8%), *M. malang* (7.8–10%), *M. mantheyi* (7.2–7.4%), *M. orientalis* (7.2–7.4%), and two undescribed lineages (MATSUI *et al.*, 2011) — *M.* "sp. 1" (7.8%) and *M.* "sp. 3" (8.3–8.4%) (Table S2).

**Vocalization.** The calls of *Microhyla kodial* (SDBDU 2017.3673) were recorded at Baikampady (the type lo-

cality), by SDB, SG, and KKV, on 6 July 2017, between 20:00–21:00 h, at air temperature: 26°C dry bulb, 24°C wet bulb. The male produced a single type of call with pulsatile temporal structure. Calls were not delivered in groups and showed uniform intervals. The mean call duration was 261.4 ms (228.6–288.3 ms) with six pulses (5–6 pulses) delivered at a rate of 18 pulses/s (17.3–18.6 pulses/s), rise time of 112.2 ms (61.8–125.6 ms), and fall time of 137.8 ms (102.3–164.1 ms). The call spectrum was characterized by a single broad peak with the overall dominant frequency of 3.8 kHz (Fig. 6; Table S4).

Acoustic comparison. The call of *Microhyla kodial* was similar to that of *M. achatina* in its duration, 261.4 ms (228.6–288.3 ms) and 228.6 ms (116.2–285.3 ms), respectively. These two species also showed a similar call rise and fall time ratio of nearly 1:1 (Fig. 6; Table S4). However, *M. kodial* differed from *M. achatina* by one of its temporal properties, i.e., slower pulse rate of 18 pulses/s, 17.3–18.6 pulses/s (vs. faster, 26.4 pulses/s, 25.6–28.5 pulses/s), and the spectral property, overall dominant frequency, which was higher at 3.8 kHz (vs. lower, 3.3 kHz) (Table S4). The various call properties of *M. achatina* observed in this study were within the range of values reported for the species (ARINI *et al.*, 2016).

On the other hand, the calls of another closely related member of *Microhyla achatina* group, *Microhyla orientalis*, were more distinct from those of *M. achatina* 



**Fig. 4.** The *Microhyla achatina* species group. **A.** Phylogenetic relationships depicted on a Maximum Likelihood phylogram based on mitochondrial 16S gene sequences from 50 samples representing six species and two undescribed lineages ("sp. 1" and "sp. 3" sensu Matsui *et al.*, 2011). Accession numbers are cross-referenced in Table S1. Numbers above and below the branches indicate Bayesian Posterior Probabilities (BPP) and RAxML bootstrap values of > 50%, respectively. **B.** Geographical locations of the morphologically examined samples in the study. **C.** Diagnostic morphological and acoustic characters for the species group.

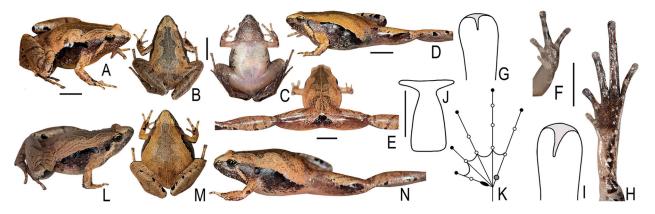
and *M. kodial*. The calls of *M. orientalis* were not only of much shorter duration, 62 ms, 48.2–67.4 ms (vs. longer, 116.2–285.3 ms for *M. achatina*; 228.6–288.3 ms for *M. kodial*), but also showed a considerably faster pulse rate of 46.5–64.5 pulses/s (vs. slower, 25.6–28.5 pulses/s for *M. achatina*; 17.3–18.6 pulses/s for *M. kodial*) (Fig. 6; Table S4; File S2). The various call properties of *M. orientalis* observed in this study were similar to those previously discussed (MATSUI *et al.*, 2013).

**Distribution and natural history.** Currently, *Microhyla kodial* is only known from two localities — Baikampady and Padil, in Mangaluru city, Karnataka state, India. Both the populations are found in highly disturbed habitats adjacent to major roadways and railway line. Animals were located at night during the months of July and August, either under grasses in a marshy area (Baikampady) or vegetation adjacent to temporary water collection sites (Padil). This species was found sympatrically with *M. ornata*. The ecology and breeding behavior of *M. kodial* was recently reported (VINEETH *et al.*, 2018) (Fig. 4).

#### Microhyla cf. heymonsi

(Figures 1–3, 8, 9, S1, S2; Tables S1–S5; File S1)

Microhyla heymonsi Vogt, 1911 was described from Taiwan, China based on eight male specimens (ZMB 54906-54913). Apart from Taiwan Island, where this species has a wide distribution (JANG-LIAW & CHOU, 2015), it is also reported from several regions across East and Southeast Asia (Cambodia, Laos, Mainland of China, Malaysia, Myanmar, Thailand, Vietnam, as well as the islands of Hainan, Singapore, and Sumatra) (Am-PHIBIAWEB, 2018; FROST, 2018). The first report of this species from South Asia was by SARKAR (1990), who reported M. heymonsi from Campbell Bay, Great Nicobar Island (India), based on a specimen collected by A. Daniel in 1966. Subsequently, the species was reported from mainland India, specifically the Northeast regions of Assam (GROSSELT et al., 2005) and Manipur (MATHEW & SEN, 2010). However, both these reports are likely to be misidentifications of M. mymensinghensis (see 'notes' under that species). For the Andaman and Nicobar popu-



**Fig. 5.** Morphological characters of *Microhyla achatina*. **A.** Dorsolateral view. **B.** Dorsal view. **C.** Ventral side. **D.** Lateral view. **E.** Posterior view of thighs. **F.** Ventral view of hand. **G.** Third finger tip. **H.** Ventral view of foot. **I.** Fourth toe tip. **J.** Terminal phalanx of fourth toe. **K.** Schematic illustration of webbing on foot (A–K, in preservation, voucher UIMZ 0031). **L.** Dorsolateral view. **M.** Dorsal view. **N.** Lateral view (L–N, in life, vouchers not preserved). Scale bars: 5 mm. (Photographs: S. D. Biju).

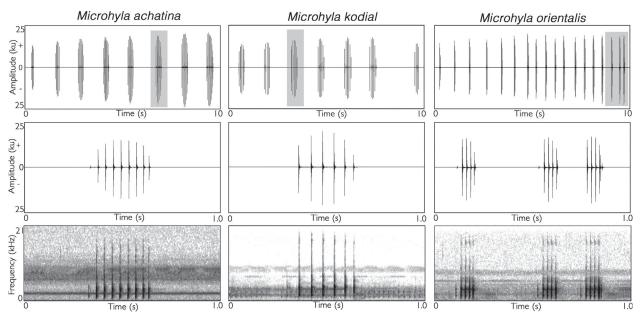


Fig. 6. Male advertisement calls of species in the *Microhyla achatina* group. Each species panel depicts (from top to bottom) oscillogram for ten-second call segment, oscillogram for 1-second call segment showing pulsatile structure, and spectrogram for 1-second call segment.

lations, although we could not examine Daniel's specimen (1966), we studied another specimen, WII-HS08 from Andaman Islands, available at WII (Dehradun, India) and identified as '*Microhyla chakrapanii*'. Our study confirmed this specimen to be a close relative of *M. heymonsi*; however, genetically the Andaman population was considerably divergent from other *M. heymonsi* populations in Southeast and East Asia (see below). Herein, we consider the Andaman populations to represent a potential candidate new species, and refer to it as *M.* cf. *heymonsi*, until further confirmation of its status. Furthermore, to facilitate future studies, we provide a description of the available specimen.

Genetic comparison. The Andaman sample of *Micro-hyla* cf. *heymonsi* is genetically close to populations

from Malaysia and Singapore with 2.1-2.7% divergence for 16S gene. Together, sub-clade 1 (Andaman + Malaysia + Singapore) differed from sub-clade 2 (Thailand + Myanmar) by 2.5-4.6% divergence; from sub-clade 3 (Laos) by 4.4-5.7% divergence; from sub-clade 4 (China + Vietnam), which is the closest to the type locality, by 4.2-6.4% divergence; from sub-clade 5 (Laos + Thailand) by 3.9-5.4% divergence; and from sub-clade 6 (Laos + Thailand) by 4.9-6.0% divergence (Fig. 8; Table S2). Our results clearly indicate that the *M. 'heymonsi*' clade represents a complex of multiple species, either representing previously available names or unrecognized diversity.

Morphological comparison. *Microhyla* cf. *heymonsi* is one of the most distinct species of South Asia and can

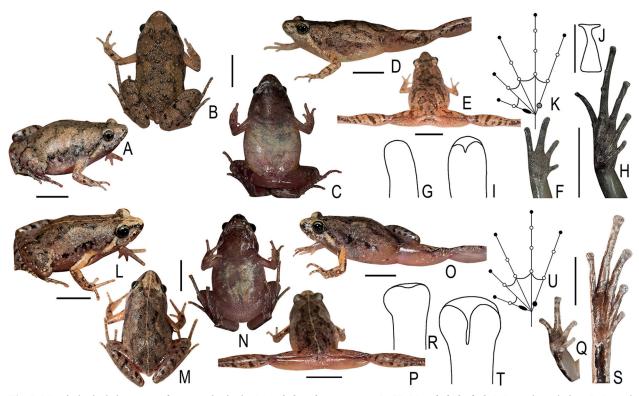


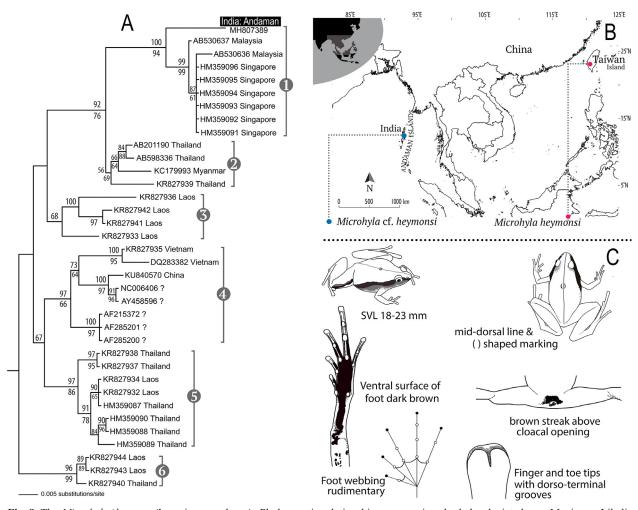
Fig. 7. Morphological characters of two species in the *Microhyla achatina* group. A–K. *Microhyla kodial*. A. Dorsolateral view. B. Dorsal view. C. Ventral view. D. Lateral view (A–D, in life, voucher SDBDU 2017.3674). E. Posterior view of thighs (in life, voucher SDBDU 2017.3675). F. Ventral view of hand. G. Third finger tip. H. Ventral view of foot. I. Fourth toe tip. J. Terminal phalanx of fourth toe. K. Schematic illustration of webbing on foot (F–K, in preservation, voucher SDBDU 2017.3674). L–U. *M. orientalis*. L. Dorsolateral view. M. Dorsal view. N. Ventral view. O. Lateral view. P. Posterior view of thighs (L–P, in life, voucher UIMZ 0037). Q. Ventral view of hand. R. Third finger tip. S. Ventral view of foot. T. Fourth toe tip. U. Schematic illustration of webbing on foot (Q–U, in preservation, voucher UIMZ 0037). Scale bars: 5 mm. (Photographs: S. D. Biju & S. Garg).

be differentiated from all other members of the region by combination of following characters: absence of webbing between toes; finger and toe discs with prominent dorsoterminal grooves, cover bifurcate distally; presence of a small '()' shaped dark marking on the center of its dorsum; a narrow mid-dorsal skin fold or line extending from the tip of snout up to the vent; and a prominent blackishbrown lateral band, marking or skin fold that starts from the tip of snout and approaches the groin (Fig. 9).

Description of WII-HS08. A small-sized adult male (SVL 20.2), slender body; head wider than long (HW 6.4, HL 5.9); snout rounded in dorsal, ventral, and lateral views, its length (SL 2.5) longer than horizontal diameter of eye (EL 1.8); loreal region acute, indistinct canthus rostralis; interorbital space flat, wider (IUE 2.0) than upper eyelid width (UEW 1.2) and internarial distance (IN 1.8); nostril oval, closer to tip of snout (NS 0.9) than eye (EN 1.2); nostril placed more towards the lateral side of the snout; supratympanic fold that extends from posterior corner of eye to shoulder present; tongue small, oval, without papillae. Arms short, forearm length (FAL 3.7) shorter than hand length (HAL 5.2); relative length of fingers I<II<IV<III (FL<sub>1</sub> 0.9, FL<sub>11</sub> 1.8, FL<sub>111</sub> 3.2, FL<sub>IV</sub> 1.9); tips of all fingers with small discs, discs with prominent dorso-terminal grooves, cover bifurcate distally; dermal fringe on fingers weakly-developed; webbing absent between fingers; subarticular tubercles rather prominent; outer palmar tubercle equal to the inner, weakly-developed; supernumerary tubercles absent; nuptial pad absent. Hind limbs short, thigh (THL 11.1) shorter than shank (SHL 12.3) and foot (FOL 12.6); distance from base of tarsus to tip of toe IV (TFOL 17.8); relative length of toes I< II< V< III< IV; toe tips dilated with-discs (TD  $_1$  0.5; TW  $_1$  0.4, TD  $_{II}$  0.6; TW  $_{II}$  0.3, TD  $_{III}$ 0.6; TW  $_{\rm III}$  0.4, TD $_{\rm IV}$  0.6, TW $_{\rm IV}$  0.4, TD $_{\rm V}$  0.5, TW $_{\rm V}$  0.3), toe discs with prominent dorso-terminal grooves, cover bifurcate distally; toes with weakly-developed dermal fringes, terminal phalanges of toes T-shaped, foot webbing almost absent: I2-2<sup>1</sup>/<sub>2</sub>II2-3III3-4IV4-3V; subarticular tubercles prominent, all present, circular; inner metatarsal tubercle prominent (IMTL 0.6), oval-shaped; outer metatarsal tubercle small (OMTL 0.4), rounded; supernumerary tubercles absent.

Skin of dorsum, lateral surfaces from head to groin, forelimbs and hind limbs (including fingers and toes) smooth to shagreened; ventral surfaces smooth (Fig. 9).

**Color in preservation (WII-HS08).** Dorsum uniformly slate grey with a light grey mid-dorsal line extending from the tip of snout to vent, a small '()' shaped dark brown marking on the center of the dorsum and mid-



**Fig. 8.** The *Microhyla 'heymonsi*' species complex. **A.** Phylogenetic relationships among six sub-clades depicted on a Maximum Likelihood phylogram based on mitochondrial 16S gene sequences from 35 samples representing *M. 'heymonsi*' from Southeast and East Asia, and one sample of *M.* cf. *heymonsi* from South Asia. Accession numbers are cross-referenced in Table S1. Numbers above and below the branches indicate Bayesian Posterior Probabilities (BPP) and RAxML bootstrap values of > 50%, respectively. **B.** Geographical location of the morphologically examined samples in the study. **C.** Diagnostic morphological characters for the clade.

dorsal line; a prominent blackish-brown lateral band or marking starting from the tip of snout and approaching the groin; forelimbs and hind limbs greyish-brown with light brown cross bands. Ventral surfaces of throat and chest light brown with minute dark brown speckles; belly light grey; margins of abdomen, forelimbs light grey with dark brown speckles; hind limbs light brown with scattered black speckles, more prominently on tibia and tarsus; foot (including toes) dark brown; a crescentshaped dark brown streak above the cloacal opening (Fig. 9).

#### Microhyla berdmorei species group

(Figures 1-3, 10, S1, S2; Tables S1-S5; File S1)

The *Microhyla berdmorei* group was proposed to include species morphologically characterized by presence of extensive foot webbing, palatines, and well-developed digital discs (DUBOIS 1987; POYARKOV *et al.*, 2014). However, this grouping is not supported phylogenetically and its various

members exhibit considerable morphological differences. Currently, we consider the Microhyla berdmorei group to comprise of a single South Asian species, M. berdmorei, based on previous reports from Bangladesh (HASAN et al., 2012) and genetic confirmation of Indian populations in the present study. Additionally, based on phylogenetic position, M. pulchra and at least one unidentified lineage (KM509166), previously misidentified as "M. rubra" (PELOSO et al., 2016) and herein referred to as Microhyla cf. berdmorei, are provisionally considered as the other Southeast and East Asian members of this group; although M. pulchra differs from M. berdmorei by lesser webbing on foot, and toe tips without discs or grooves (Figs. 1, 10); and M. cf. berdmorei differs from both M. berdmorei and M. pulchra by considerably high genetic divergence of 7.9-10.4% and 10.2-13%, respectively (Table S2).

Based on unconfirmed reports, *Microhyla pulchra* was reported to occur in the Northeast regions of India (DINESH *et al.*, 2009). This could be due to erroneous citing of a report of *Kaloula pulchra* (DEY & GUPTA, 2001 "2000") on the amphibian species of the world database

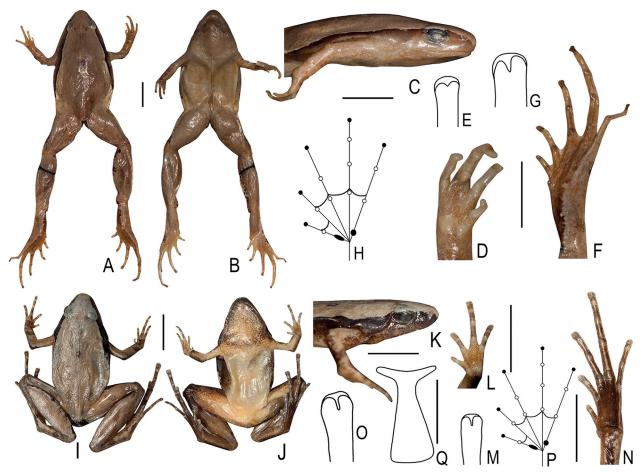


Fig. 9. Morphological characters of *Microhyla heymonsi* and *M.* cf. *heymonsi*. A–H. *Microhyla heymonsi* (in preservation, voucher ZMB 54906, syntype, an adult male, SVL 22.3 mm). A. Dorsal view. B. Ventral view. C. Lateral view of head. D. Ventral view of hand. E. Third finger tip. F. Ventral view of foot. G. Fourth toe tip. H. Schematic illustration of webbing on foot. I–P. *Microhyla* cf. *heymonsi* (in preservation, voucher WIIHS08, an adult male). I. Dorsal view. J. Ventral view. K. Lateral view of head. L. Ventral view of hand. M. Third finger tip. N. Ventral view of foot. O. Fourth toe tip. P. Schematic illustration of webbing on foot. Q. Terminal phalanx of fourth toe. Scale bars: 5 mm. (Photographs: S. D. Biju).

(FROST, 2004; CHRISTY *et al.*, 2007), which was probably followed in a checklist by DINESH *et al.* (2009). However, during our study, we have not located this species either in potential museums such as ZSIC (Kolkata, India), NERC-ZSI (Shillong, India), and NHM (London), or during field surveys across India, especially the Northeastern states. Hence, we consider the occurrence of *M. pulchra* in India to be doubtful.

#### Microhyla berdmorei Blyth, 1856 "1855"

Pegu Rice Frog (FRANK & RAMUS, 1995)

(Figures 1-3, 10, S1, S2; Tables S1-S5; File S1)

**Original name and description.** Engystoma (?) berdmorei Blyth E., 1856 "1855". Report for October Meeting 1855, Journal of the Asiatic Society of Bengal 24: 720. **Type.** Not stated. **Type locality.** "Pegu" (= Bago), Myanmar. **Current status of specific name.** Valid name, as Microhyla berdmorei (Blyth, 1856 "1855") (PARKER, 1934). **Diagnosis.** A large-sized species (male SVL 33-36 mm, N=6); snout rounded to sub-ovoid in dorsal and ventral views, nearly rounded in lateral view; tympanic fold absent; finger tips with weakly-developed discs with or without dorso-terminal grooves; toe tips expanded into discs with dorso-terminal grooves and cover bifurcate distally; terminal phalanges of toes Y-shaped; inner metatarsal tubercles, oval, and outer metatarsal tubercles, rounded; presence of a faint or discontinuous mid-dorsal skin fold; dorsal skin shagreened with scattered tubercles; lateral surfaces lighter in color with discontinuous lateral markings, band or skin fold; groin and ventral surface of thighs greenish-yellow colored in life; dorsal surface of forelimbs and hindlimbs with prominent to faint crossbands; light or dark brown patch above the cloacal opening, either of various sizes and shapes (inverted-U or crescent-shaped) or spots on either side of the cloaca.

Morphological comparison. *Microhyla berdmorei* can be differentiated from all other known *Microhyla* species presently recognized from South Asia by its large

foot webbing, extending well beyond the first subarticular tubercle on either side of toe IV and up to the discs on the remaining toes (vs. rudimentary to medium foot webbing in all other species); terminal phalanges of toes Y-shaped (vs. simple, knobbed, or T-shaped in all other species); toes tips enlarged into discs with dorso-terminal grooves and cover bifurcate distally (vs. absent, except in M. kodial, M. cf. heymonsi, and the Microhyla zeylanica group); presence of a faint or discontinuous mid-dorsal skin fold (vs. prominent, except in M. kodial); and lateral surfaces with discontinuous markings, band or skin fold (vs. prominent, except in M. kodial). Further, it differs from M. kodial and members of the Microhyla zeylanica group by its relatively larger adult size, male SVL 33-36 mm (vs. smaller, male SVL 14-19 mm in M. kodial; male SVL 13–20 mm for *Microhyla zeylanica* group); and from M. cf. heymonsi by absence of '()' shaped marking on the mid-dorsum (vs. present). This species can be differentiated from its close genetic congener, M. pulchra, by presence of toe discs with dorso-terminal grooves (vs. absent); large foot webbing, extending beyond the first subarticular tubercle on either side of toe  $IV, I1 - 1II1 - 1^{+}III1 - 1^{1/}_{2}IV1^{1/}_{2} - 1V$  (vs. small, below the second subarticular tubercle on either side of toe IV, I1<sup>+</sup>- $2^{+}II1^{2}/_{3}-3^{-}III2^{1}/_{2}-4^{-}IV4^{-}-2^{4}/_{5}V$ ; and absence of striking dorsal markings (vs. presence of numerous undulating bands and spots on the dorsum).

Genetic comparison. The average uncorrected sequence divergence between Microhyla berdmorei and all other available homologous 16S sequences for the Microhyla berdmorei group was ≥7.3%. However, phylogenetically, M. berdmorei was closely related to M. pulchra (7.3-12.3%) and an unidentified lineage M. cf. berdmorei (7.9-10.4%). Intraspecific genetic distances within the M. berdmorei clade were also considerably high (up to 5.2%) suggesting that it could be a complex of multiple species, comprising of either undescribed diversity, other valid species such as M. darevskii (from Vietnam, Po-YARKOV et al., 2014), or previously available names from Thailand such as M. fowleri TAYLOR, 1934 and M. malcolmi COCHRAN, 1927 currently in its synonymy. However, the Indian populations were more closely related to populations from Bangladesh and Myanmar (the country of its original description) (Fig. 10; Table S2).

**Distribution and natural history.** This species is widely distributed in Asia, mainly regions in China, Myanmar, Thailand, Laos, Vietnam, Cambodia, Malaysia, Indonesia, Bangladesh, and India (FROST, 2018). The species was reported from South Asian regions in Bangladesh (MAHONY *et al.*, 2009; HASAN *et al.*, 2012). In India, it was reported from several Northeast states (e.g., MANTHEY & GROSSMANN, 1997; DEVI & SHAMUNGOU, 2006; MATHEW & SEN, 2010); however, without genetic confirmation. In this study, we confirm the presence of *M. berdmorei* in the Northeast states of Assam, Meghalaya, and Tripura, based on new molecular and morphological data (Fig. 10). The new populations were sampled from low

lying areas close to thickly vegetated water bodies either inside secondary forests or adjacent to human settlements. Breeding activity was observed in Assam during the months of October–November.

Taxonomic remark. The status of type specimens of this nominal taxon remains confusing. Three specimens available at ZSI Kolkata (India), ZSI 9718 (SVL 35.2 mm), ZSI 9719 (SVL 32.2 mm), and ZSI 9720 (SVL 33.3 mm) from "Arakan" (Myanmar) that refer to this species are currently in poorly preserved condition. Anderson (1871) listed these specimens as types and this was followed by Sclater (1892). However, Theobald (1873) commented that specimens from "Arakan" cannot be the types of this species since the syntypes were collected from Schwe Gyen (= Shwegyin) by Major Berdmore, based on available records (THEOBALD, 1873; CHANDA, DAS & DUBOIS, 2000). We examined the available specimens (ZSI 9718-ZSI 9720) and found them to largely match with the original description and our newly sampled populations.

Another taxon, *Microhyla fowleri* Taylor, 1934 described from "Chieng Mai, Siam" (= Thailand) is currently under the synonymy of *M. berdmorei* (e.g., BOURRET, 1942; TAYLOR, 1962). This taxon was removed from the synonymy of *M. berdmorei* (DUBOIS, 1987), but placed back by MATSUI *et al.* (2011). Subsequently, POYARKOV *et al.* (2014) discussed the taxonomic history and recognized *M. fowleri* as a valid species; however, without providing additional evidence for their decision. Although, we could not examine the type specimen of *M. fowleri* (ANSP 19903), our molecular analysis shows some divergent populations from neighboring regions in Southeast Asia (Indonesia and Malaysia) that require further morphological studies to confirm whether or not they refer to *M. fowleri*.

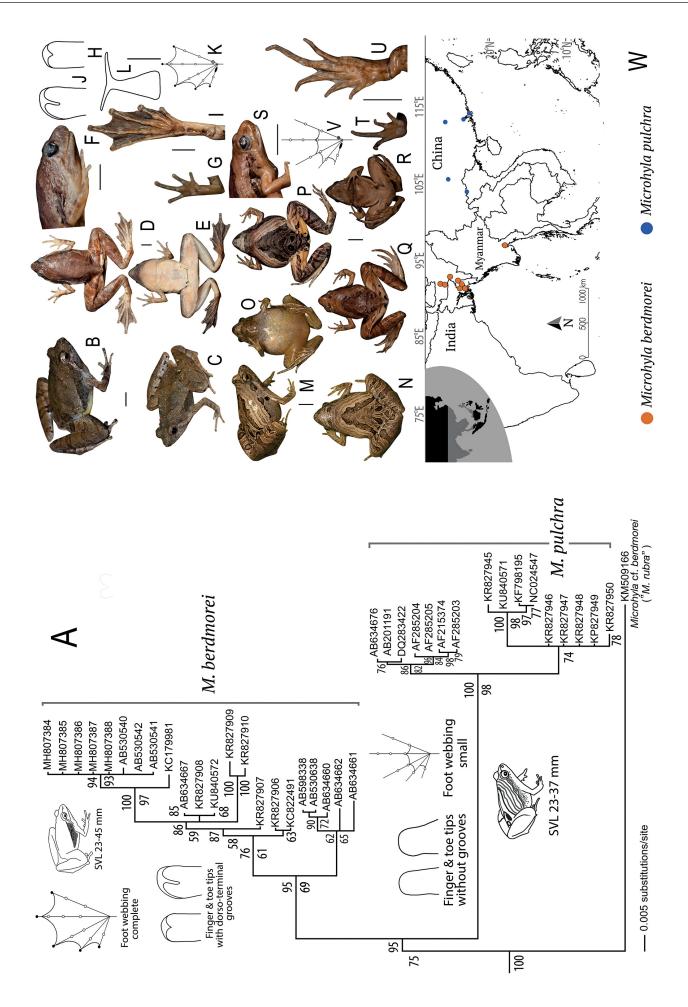
**Note.** Another species, *Microhyla butleri* was reported from Mizoram with a snout-vent size of "SVL 31–34 mm", without any information on vouchers or the sex (LALREMSANGA *et al.*, 2007). Based on the previously reported size range for *M. butleri*, male SVL 20–25 mm, female SVL 21–26 mm (POYARKOV *et al.*, 2014), this record could be a misidentification and is likely to correspond to *M. berdmorei* (male SVL 33–36 mm) or an undescribed species in the *Microhyla berdmorei* group.

#### Microhyla fissipes species group

(Figures 1-3, 11-15, S1, S2; Tables S1-S5; Files S1, S2)

**Members included.** South Asia — *Microhyla chakrapanii*, *M. mukhlesuri*, and *M. mymensinghensis*; East and Southeast Asia — *M. fissipes*, *M. mixtura*, and *M. okinavensis*.

**Diagnosis.** The group is distinguished from other *Microhyla* groups of South Asia by the following suite of morphological characters: small to medium-sized adults



two known and an undescribed lineage. Diagnostic morphological characters are depicted alongside the clades. Accession numbers are cross-referenced in Table S1. Numbers above and below the branches M. Dorsolateral view. N. Dorsal view. O. Ventral view (M-O, in life, not preserved). P. Dorsolateral view (in preservation, voucher CIB 103704). Q. Dorsolateral view. R. Ventral view. S. Lateral view of → Fig. 10. The Microhyla berdmorei species group. A. Phylogenetic relationships depicted on a Maximum Likelihood phylogram based on mitochondrial 16S gene sequences from 39 samples representing ndicate Bayesian Posterior Probabilities (BPP) and RAXML bootstrap values of > 50%, respectively. B-L. Morphological characters of Microhyla berdmorei. B. Dorsolateral view (in life, voucher WII nead. T. Ventral view of hand. U. Ventral view of foot. V. Schematic illustration of webbing on foot (Q-V, in preservation, voucher CIB 68624). W. Geographical distribution of *M. berdmorei* in India based C. Dorsolateral view (in life, voucher WII ADA 5227). D. Dorsal view. E. Ventral view of head. G. Ventral view of hand. H. Third finger tip. I. Ventral view of foot. J. Fourth toe tip. K. Schematic illustration of webbing on foot (D-K, in preservation, voucher WII ADA 5227). L. Terminal phalanx of fourth toe (voucher SDBDU 2009.439). M-V. Morphological characters of M. pulchra. genetically confirmed samples, and distribution of *M. pulchra* in China based on morphologically studied samples. Scale bars: 5 mm. (Photographs: S. D. Biju; B–C, A. Das; M–O, J. Jiang). uc (male SVL 17–25 mm, female SVL 22–28 mm); nostrils placed towards the lateral sides of the snout; finger and toe tips rounded or having small discs without grooves; terminal phalanges of toes knobbed or T-shaped; inner metatarsal tubercle present, elongate; outer metatarsal tubercle small, rounded; webbing between toes absent or rudimentary; dorsal skin shagreened to sparsely granular; a narrow mid-dorsal skin fold or line extending from tip of the snout to the vent; a streak (white or light brown in life, and grey in preservation) extending from posterior corner of the eye to the shoulder; and a prominent dark lateral band, marking, or skin fold starting from tip of the snout or nostril and approaching the groin on either side of the body (Fig. 11).

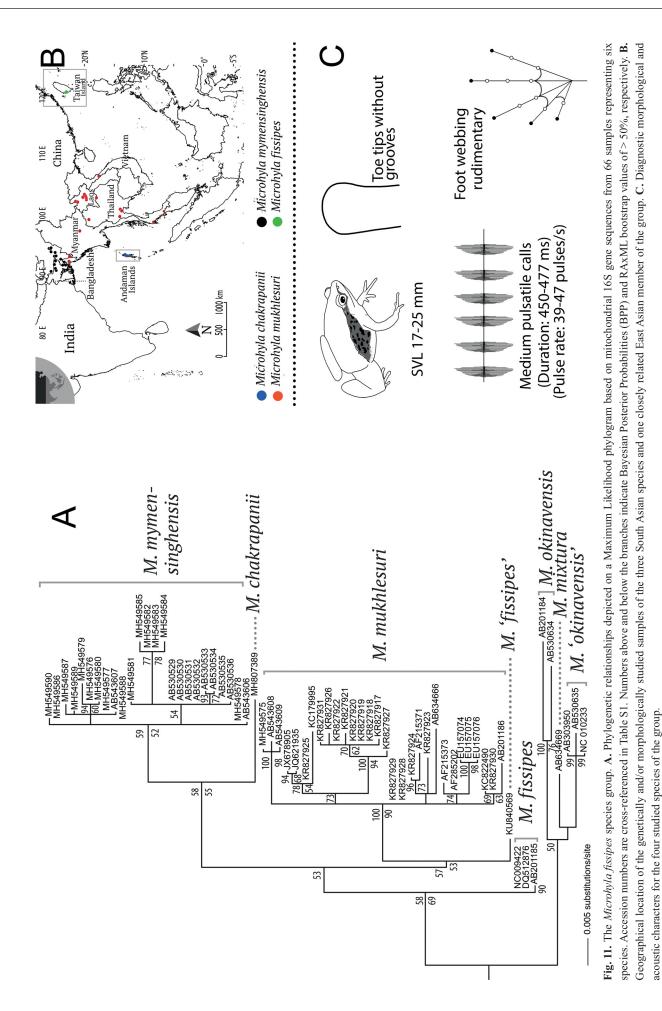
**Morphological comparison.** Species in this group differ from members of *Microhyla achatina* group by their toe tips having small discs without grooves (vs. toe discs with prominent dorso-terminal grooves and cover bifurcate distally); from *Microhyla zeylanica* group by relatively larger adult size, male SVL 17–25 mm, female SVL 22–28 mm (vs. smaller, male SVL 13–20 mm, female SVL 15–23 mm), nostrils placed towards the lateral sides of the snout (vs. more towards the dorsal side of the snout), and toe tips having small discs without grooves (vs. discs with circum-marginal grooves in *Microhyla zeylanica*, and prominent dorso-terminal grooves with cover bifurcate distally in the remaining species); from *Microhyla ornata* group by toe tips with small discs (vs. rounded without discs), and weakly-developed outer metatarsal tubercles (vs. relatively well-developed); from *Microhyla rubra* group by toe tips having small discs (vs. rounded without discs), terminal phalanges of toes knobbed or Y-shaped (vs. simple with rounded tips), and inner and outer metatarsal tubercles small, rounded, not shovel-shaped (vs. large and shovel-shaped).

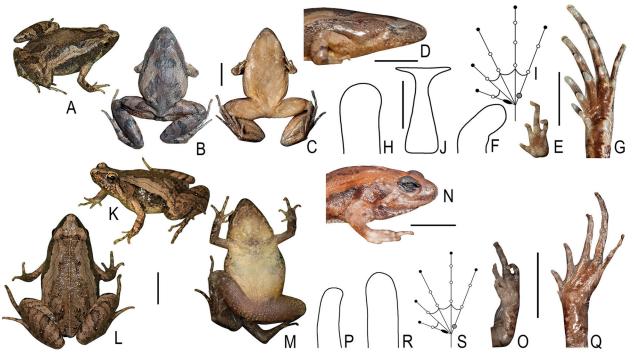
**Genetic relationships.** Phylogenetically, *Microhyla fissipes* group is the most inclusive clade containing *M. chakrapanii*, *M. fissipes*, *M. mixtura*, *M. mukhlesuri*, *M. mymensinghensis*, and *M. okinavensis*, but none of the other clades that have been genetically studied so far within the entire radiation of *Microhyla* (Figs. 1, 11).

The previously unassigned *M. chakrapanii* was found sister to *M. mymensinghensis* with high support within this group (Fig. 1) and together the two were closely related to *M. mukhlesuri*, with *M. fissipes* being basal to all three species in the combined mt + nu as well as the independent mt analyses (Figs. 1, 11). This relationship was not congruent with previous mitochondrial phylogenies that found *M. mukhlesuri* as the sister species of *M. fissipes* and together they formed a sister relation with *M. mymensinghensis* (e.g., HASAN *et al.*, 2012, 2014A; HOWLADER *et al.*, 2016; YUAN *et al.*, 2016). Sequences representative of two other species, *M. mixtura* + *M. okinavensis*, were consistently recovered as the basal taxa in this group (e.g., MATSUI *et al.*, 2011; HOWLADER *et al.*, 2016). For detailed discussion on intra- and interspecific pairwise divergence see the respective 'species' accounts and Table S2.

**Acoustic comparison.** Species in this group can be differentiated from the other *Microhyla* groups of South Asia by their medium-sized pulsatile calls. The calls of two studied species in this group, *M. mymensinghensis* and *M. fissipes*, showed structural resemblance with members of the *Microhyla ornata* group, however, they differed in temporal properties such as call duration and pulse rate. *Microhyla fissipes* call also showed structural similarities with members of the *Microhyla achatina* group, but differed in temporal properties such as the number of pulses and pulse rate (Fig. 13; Table S4). For comparison between *M. mymensinghensis* and *M. fissipes* calls from China and Thailand, see File S2.

**Note.** Members of *Microhyla fissipes* group in South Asia share several metric and meristic characters with members of the *Microhyla ornata* group (see diagnosis), and most species of the *Microhyla fissipes* group (e.g., *M. fissipes*, *M. mukhlesuri*, *M. my-mensinghensis*, and *M. okinavensis*) were also previously misidentified as *M. ornata* (MATSUI *et al.*, 2005; GARG *et al.*, 2018A). However, phylogenetically the three South Asian members, *M. chakrapanii*, *M. mukhlesuri*, and *M. mymensinghensis* are nested along with *M. fissipes*, and together these four species show a sister relationship with





**Fig. 12.** Morphological characters of two species in the *Microhyla fissipes* species group. **A**–**J**. *Microhyla chakrapanii*. **A**. Dorsolateral view (in life, not preserved). **B**. Dorsal view. **C**. Ventral view. **D**. Lateral view of head. **E**. Ventral view of hand. **F**. Third finger tip. **G**. Ventral view of foot. **H**. Fourth toe tip. **I**. Schematic illustration of webbing on foot. **J**. Terminal phalanx of fourth toe (B–J, in preservation, voucher WII HC184). **K**–**S**. *M. fissipes*. **K**. Dorsolateral view. **L**. Dorsal view. **M**. Ventral view (in life, not preserved). **N**. Lateral view of head. **O**. Ventral view of hand. **P**. Third finger tip. **Q**. Ventral view of foot. **R**. Fourth toe tip. **S**. Schematic illustration of webbing on foot (N–S, in preservation, voucher CIB 68500). Scale bars: 5 mm. (Photographs: S. D. Biju; A, S. Harikrishnar; K–M, J. Jiang).

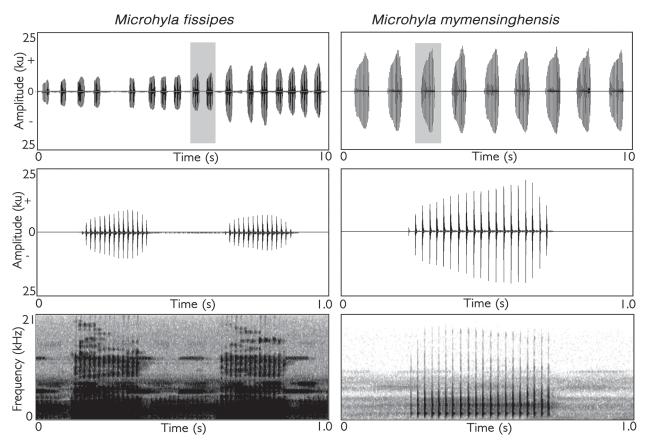
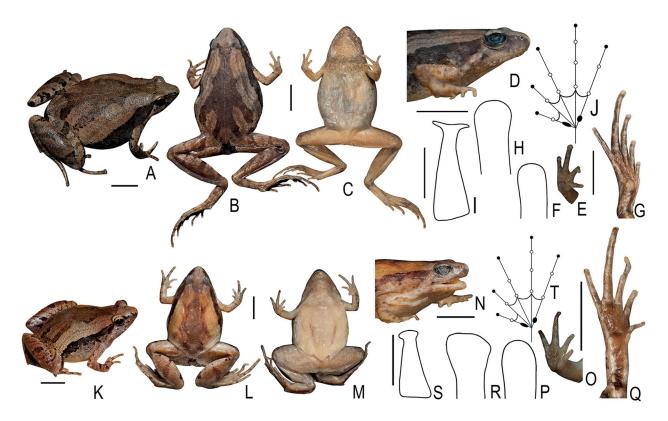


Fig. 13. Male advertisement calls of two species in the *Microhyla fissipes* species group. Each species panel depicts (from top to bottom) oscillogram for ten-second call segment, oscillogram for 1-second call segment showing pulsatile structure, and spectrogram for 1-second call segment.



**Fig. 14.** Morphological characters of two species in the *Microhyla fissipes* species group. **A–J.** *Microhyla mukhlesuri*. **A.** Dorsolateral view (in life, voucher SDBDU 2010.1339a). **B.** Dorsal view. **C.** Ventral view. **D.** Lateral view of head. **E.** Ventral view of hand. **F.** Third finger tip. **G.** Ventral view of foot. **H.** Fourth toe tip. **I.** Terminal phalanx of fourth toe. **J.** Schematic illustration of webbing on foot (B–J, in preservation, voucher SDBDU 2010.1334). **K–T.** *M. mymensinghensis*. **K.** Dorsolateral view (in life, voucher WIII ADA 50B). **L.** Dorsal view. **M.** Ventral view. **N.** Lateral view of head. **O.** Ventral view of hand. **P.** Third finger tip. **Q.** Ventral view of foot. **R.** Fourth toe tip. **S.** Terminal phalanx of fourth toe. **T.** Schematic illustration of webbing on foot (L–S, in preservation, voucher WIII ADA 50B). Scale bars: 5 mm. (Photographs: S. D. Biju).

the clade containing *M. mixtura* and *M. okinavensis*. Therefore, currently we include all the six species in the *Microhyla fissipes* group, although further studies based on robust phylogenies combined with morphological and acoustic evidence could provide more insights on this grouping.

Specifically, the South Asian members (*Microhyla chakrapanii*, *M. mukhlesuri*, and *M. mymensinghensis*) differ from *M. okinavensis* and *M. mixtura* by absence of dorso-terminal grooves on toes (vs. present) (Fig. 15); and specifically differ from *M. mixtura* by absence of prominent oval blotches on dorsum and elongate dark brown markings on lateral surfaces (vs. present). However, *M. fissipes* is morphologically more closely related to the three South Asian species.

#### Microhyla chakrapanii Pillai, 1977

Chakrapani's Narrow-mouthed Frog (Das & DUTTA, 1998) (Figures 1–3, 11, 12, S1, S2; Tables S1–S5; File S1)

**Original name and description.** *Microhyla chakrapanii* Pillai, R. S. 1977. On two frogs of the family Microhylidae from Andamans including a new species. *Proceedings of the Indian Academy of Sciences, Section*  *B* 86: 135–138. **Type.** Holotype ZSI-SRS VA/770. **Type locality.** "Mayabunder (east of Burma temple), North Andamans", India. **Current status of specific name.** Valid name, as *Microhyla chakrapanii* Pillai, 1977.

Morphological comparison. Microhyla chakrapanii could be confused with M. fissipes, M. mixtura, M. mukhlesuri, M. mymensinghensis, and M. okinavensis within the Microhyla fissipes group. However, M. chakrapanii differs from M. mukhlesuri by its relatively smaller adult size, male SVL 17-22 mm, N=5 (vs. larger, male SVL 23-25 mm, N=4), upper eyelid width equal to the internarial distance, UEW 1.2-1.4 mm, IN 1.2-1.4, N=5 (vs. shorter, UEW 1.2-1.3 mm, IN 1.8-1.9, N=4), and terminal phalanges of toes T-shaped with prominently expanded lateral processes (vs. T-shaped with moderately expanded lateral processes); and from M. mymensinghensis by its upper eyelid width equal to the internarial distance, UEW 1.2–1.4 mm, IN 1.2–1.4, N=5(vs. shorter, UEW 1.1-1.4 mm, IN 1.5-1.8, N=6), and terminal phalanges of toes T-shaped with prominently expanded lateral processes (vs. knobbed with slight lateral expansion). For comparison with Microhyla fissipes, M. mixtura, and M. okinavensis see 'Note' under Microhyla fissipes group.

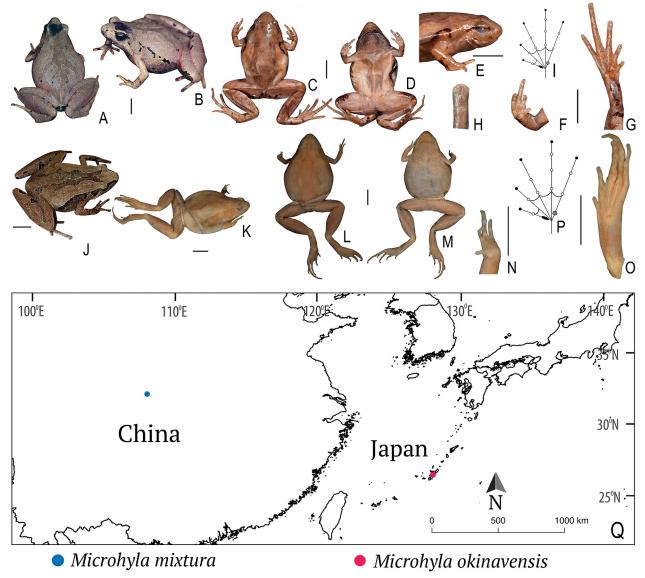


Fig. 15. Two East and Southeast Asian members of the *Microhyla fissipes* species group. A–I. *Microhyla mixtura*. A. Dorsal view. B. Dorsolateral view (in life, not preserved). C. Dorsal view. D. Ventral view. E. Lateral view of head. F. Ventral view of hand. G. Ventral view of foot. H. Fourth toe tip. I. Schematic illustration of webbing on foot (C–I, in preservation, voucher CIB 65706). J–P. *Microhyla okinavensis*. J. Dorsolateral view (in life, not preserved). K–P. Holotype (USNM 36553). K. Dorsolateral view. L. Dorsal view. M. Ventral view. N. Ventral view of hand. O. Ventral view of foot. P. Schematic illustration of webbing on foot. Q. Geographical locations of the morphologically examined samples of *M. mixtura* and *M. okinavensis* in the study. Scale bars: 5 mm. (Photographs: S. D. Biju; A–B, J. Jiang; K–O, J. Poindexter).

**Genetic comparison.** Phylogenetic results recovered *Microhyla chakrapanii* as sister taxon to *M. mymensin-ghensis* (Figs. 1, 11) from which it differs by relatively low uncorrected genetic distances of 2.3-3.1% for the 16S gene. This species differs from other closely related species *M. fissipes* and *M. mukhlesuri* by distances of 2.9% and 3.7-6.2%, respectively (Table S2).

**Distribution and natural history.** *Microhyla chakrapanii* is presently restricted to Andaman Islands (India). This species was originally reported from Mayabunder on the Middle Andaman Island (PILLAI, 1977) and subsequently reported from South Andaman Island (CHANDRAMOULI *et al.*, 2011) and the Long Island (HARIKRISHNAN *et al.*, 2012). Animals have mostly been found under grasses on the edges of temporary pools and puddles predominantly in secondary forests during the breeding season (mostly in November). The species is also reported to occur in paddy fields and primary evergreen forests, and description of its advertisement call, eggs, and tadpoles are available (CHANDRAMOULI *et al.*, 2011, 2015).

**Note.** Due to close resemblance of *Microhyla chakrapanii* with *M. achatina*, *M. heymonsi*, *M. palmipes*, and *M. superciliaris* (DUTTA, 1997), this species was placed in the *Microhyla achatina* group (CHANDA, 2002). However, our study confirms the close relation of *M. chakrapanii* with members of the *Microhyla fissipes* group based on

molecular and morphological evidence (Figs. 1, 11, 12). Future acoustic studies could be useful for understanding the distinctiveness of this species from closely related congeners.

## *Microhyla mukhlesuri* Hasan, Islam, Kuramoto, Kurabayashi & Sumida, 2014

Mukhlesur's Narrow-mouthed Frog

(Figures 1-3, 11, 14, S1, S2; Tables S1-S5; File S1)

**Original name and description.** *Microhyla mukhlesuri* Hasan M. K., Islam M. M., Kuramoto M., Kurabayashi A. & Sumida M. 2014. Description of two new species of *Microhyla* (Anura: Microhylidae) from Bangladesh, *Zootaxa* 3755: 401–408. **Type.** Holotype IABHU 3956, by original designation. **Type locality.** "Raozan, Chittagong (22° 35' N, 91° 55' E, > 9 m asl.), Bangladesh". **Current status of specific name.** Valid name, as *Microhyla mukhlesuri* Hasan, Islam, Kuramoto, Kurabayashi & Sumida, 2014.

**Description of holotype.** A detailed description is available (Hasan *et al.*, 2014A).

Morphological comparison. Microhyla mukhlesuri could be confused with M. chakrapanii, M. fissipes, M. mixtura, M. mymensinghensis, and M. okinavensis within the Microhyla fissipes group. However, M. mukhlesuri differs from M. mymensinghensis by its relatively larger adult size, male SVL 23-25 mm, N=4 (vs. smaller, male SVL 20–24 mm, N=6), and terminal phalanges of toes T-shaped with moderately expanded lateral processes (vs. knobbed with slight lateral expansion). Diagnostic characters, e.g., finger length and marking on the anus (HASAN et al., 2014A), could not be confirmed as we found them to be variable among the examined specimens. Differences with M. chakrapanii are provided in the comparison section of that species and for comparison with M. fissipes, M. mixtura, and M. okinavensis see 'Note' under Microhyla fissipes group.

Genetic comparison. Phylogenetically, Microhyla mukhlesuri is closely related to M. chakrapanii, M. fissipes, and M. mymensinghensis (Figs. 1, 11) and differs from them by uncorrected genetic distances of 3.7-6.2%, 1.4-3.3%, and 2.8-5.4%, respectively, for the 16S gene (Table S2). The Indian population of *M. mukhlesuri* was genetically similar to the populations from Bangladesh (the country of its original description) (Fig. 11). However, the intraspecific genetic distances within the entire M. mukhlesuri clade were as high as 3.3% (Table S2). The highest divergence was observed between the subclade of Bangladesh (typical) + Indian sample with populations from geographically distant regions such as Laos in Southeast Asia, where the distribution ranges of M. mukhlesuri and *M. fissipes* are shown to be closely demarcated (YUAN et al., 2016). Hence, further studies will be necessary to

understand the patterns of genetic differentiation within the *M*. '*fissipes*'-*M*. *mukhlesuri* complex.

**Distribution and natural history.** *Microhyla mukhlesuri* was originally reported from Raozan, Chittagong District, in southeastern Bangladesh (HASAN *et al.*, 2014A). Subsequently, it was reported from the Mizoram state of Northeast India (GARG *et al.*, 2018A). This species has been found under grasses on edges of water bodies (HASAN *et al.*, 2014A) in Bangladesh. Based on other available 16S sequences (Table S1) and the recent study by YUAN *et al.* (2016), *M. mukhlesuri* also has a wide distribution in Southeast Asia (Malaysia, Myanmar, Laos, Thailand, and Vietnam).

#### Microhyla mymensinghensis Hasan, Islam, Kuramoto, Kurabayashi & Sumida, 2014

Mymensingh Narrow-mouthed Frog

(Figures 1–3, 11, 13, 14, S1, S2; Tables S1–S5; File S1)

**Original name and description.** *Microhyla mymensinghensis* Hasan M. K., Islam M. M., Kuramoto M., Kurabayashi A. & Sumida M. 2014. Description of two new species of *Microhyla* (Anura: Microhylidae) from Bangladesh, *Zootaxa* 3755: 401–408. **Type.** Holotype IAB-HU 4116, by original designation. **Type locality.** "Bangladesh Agricultural University Campus (24° 44' 50" N, 90° 24' 24" E, > 18 m asl.), Mymensingh, Bangladesh". **Current status of specific name.** Valid name, as *Microhyla mymensinghensis* Hasan, Islam, Kuramoto, Kurabayashi & Sumida, 2014.

**Description of holotype.** A detailed description is available (HASAN *et al.*, 2014A).

**Morphological comparison.** *Microhyla mymensinghensis* could be confused with *M. chakrapanii*, *M. fissipes*, *M. mixtura*, *M. mukhlesuri*, and *M. okinavensis* within the *Microhyla fissipes* group. Of these, it is morphologically cryptic with *M. chakrapanii* and *M. mukhlesuri*; for differences see their respective comparison sections. Some of the diagnostic characters mentioned in the original description (e.g., size and markings around the cloacal region) were found to be overlapping or variable in the examined specimens. For differences with *M. chakrapanii* see comparison section of that species and for comparison with *M. fissipes*, *M. mixtura*, and *M. okinavensis* see 'Note' under *Microhyla fissipes* group.

**Genetic comparison.** Phylogenetically, *Microhyla mymensinghensis* is sister taxon to *M. chakrapanii* (Figs. 1, 11), from which it was found to differ by uncorrected genetic distances of 2.3-3.1% for the 16S sequences. This species differs from other closely related species *M. fissipes* and *M. mukhlesuri* by distances of 2.7-3.7% and 2.8-5.4%, respectively (Table S2). Within the *M. mymensinghensis* clade, populations from Nagaland were divergent by 1.4–2.1%, indicating the need for further studies to gain insights into the patterns of genetic differentiation within and among closely related species of the *Microhyla fissipes* group.

**Vocalization.** The calls of *Microhyla mymensinghensis* (SDBDU 2015.2905) were recorded at Mandia, Assam, by SDB and SG, on 13 June 2015, between 19:00-20:00 h, at air temperature:  $26.5^{\circ}$ C dry bulb,  $26.0^{\circ}$ C wet bulb. The male produced a single type of call with pulsatile temporal structure and the calls were not delivered in groups. The mean call duration was 466.4 ms (450.2-477.1 ms) with 21 pulses (19-22 pulses) delivered at a rate of 43.1 pulses/s (39.0-47.2 pulses/s), rise time of 333.4 ms (280.1-370.4 ms), and a short fall time of 79.8 ms (68.8-102.6 ms). The call spectrum was characterized by two broad peaks with mean dominant frequency of 3.6 kHz (Fig. 13; Table S4).

Acoustic comparison. Among members of the *Microhyla fissipes* group, we compared the call of *Microhyla mymensinghensis* with new call recordings of *M. fissipes* (Fig. 13) from China and the previously published calls of *M. fissipes* populations from Thailand (published as '*M. ornata*' by HEYER, 1971). The calls of *M. mymensinghensis* were longer in duration, 450.2–477.1 ms (vs. shorter in both populations of *M. fissipes*, 230–310 ms) with a slower pulse rate, 39.0–47.2 pulses/s (vs. faster in both populations of *M. fissipes*, 53.0–63.0 pulses/s). The overall structure of *M. mymensinghensis* call also had resemblance with members of the *Microhyla ornata* group. However, *M. mymensinghensis* had relatively longer calls, 450.2–477.1 ms (vs. shorter, 321.1–378.6 ms in *M. ornata*, and 311.3–368.7 ms in *M. nilphamariensis*).

Distribution and natural history. Microhyla mymensinghensis was originally described from Mymensingh in Bangladesh. Subsequently, this species was shown to be widely distributed in northeast regions of India, with genetically confirmed records from the states of Assam, Manipur, Meghalaya, Nagaland, Tripura, and West Bengal (GARG et al., 2018A). In India, specimens were usually found at night either on pond edges inside secondary forest patches or along slow moving streams (Nagaland, Meghalaya, and Tripura). In Assam and Manipur, we located individuals under grasses or leaf litter 1-2 m away from riverbanks. This species was also fairly common outside forested areas, including human settlements and temporary roadside puddles (Assam and Nagaland) (Fig. 11). A calling population observed on the edges of a temporary roadside water puddle in Assam was recorded for the study.

**Note.** *Microhyla heymonsi* was reported from Assam along with description of its call (GROSSELT et al., 2005), however, without any voucher information. Based on the call properties, we suggest it corresponds to *M. my-mensinghensis*. We also collected *M. mymensinghensis* from a nearby locality of Assam (Maruacherra, Cachar),

supporting the misidentification. Another population of *M. heymonsi* was reported from Manipur (MATHEW & SEN, 2010), however the accompanying photographs correspond to *M. mymensinghensis*.

#### Microhyla ornata species group

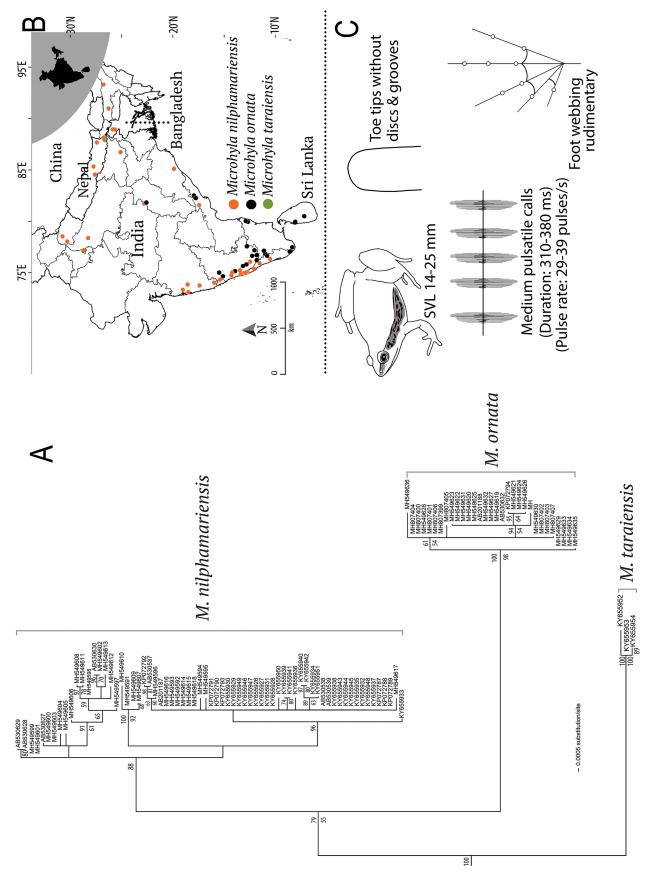
(Figures 1-3, 16-19, S1, S2; Tables S1-S5; File S1)

**Members included.** South Asia — *Microhyla nilphamariensis, M. ornata*, and *M. taraiensis.* 

**Diagnosis.** The group is distinguished from other *Microhyla* groups of South Asia by the following suite of characters: small to medium-sized adults (male SVL 15–24 mm, female SVL 22–28 mm); nostrils placed towards the lateral sides of the snout; finger and toe tips rounded without discs and grooves; terminal phalanges of toes T-shaped; distinct inner and outer metatarsal tubercles; dorsal skin shagreened to granular; foot webbing small; presence of a narrow mid-dorsal skin fold or line extending from tip of the snout to the vent; presence of a prominent dark blackish-brown lateral band, marking, or skin fold starting from tip of the snout or nostril and approaching the groin on either side of the body (Figs. 16, 17).

Morphological comparison. Species in this group differ from the Microhyla rubra group by terminal phalanges of toes T-shaped (vs. simple with rounded tips), inner and outer metatarsal tubercles not shovel-shaped (vs. shovel-shaped), small foot webbing, not beyond the third subarticular tubercle on either side of toe IV (vs. more, extending beyond the second subarticular tubercle), and dorsum with prominent reticulations and markings (vs. reddish-brown without prominent markings); from the Microhyla zeylanica group by relatively larger adult size, male SVL 15-24 mm, female SVL 22-28 mm (vs. smaller, male SVL 13–20 mm, female SVL 15–23 mm), nostrils placed towards the lateral sides of the snout (vs. more towards the dorsal side of the snout), and toe discs without grooves (vs. with circum-marginal grooves in *M. zeylanica*, or with prominent dorso-terminal grooves and cover bifurcate distally in other species) (Fig. 16). For differences with the Microhyla achatina group, Microhyla berdmorei group, and Microhyla fissipes group, see their comparison sections.

**Genetic relationships.** Phylogenetically, the *Microhy-la ornata* group is the most inclusive clade containing *Microhyla nilphamariensis*, *M. ornata*, and *M. taraiensis*, but none of the other clades that have been phylogenetically studied so far within the entire radiation of *Microhyla* (Fig. 1). In the mt 16S analysis, we recovered the recently described *Microhyla taraiensis* as the sister species of *M. nilphamariensis* + *M. ornata* as shown previously (KHATIWADA *et al.*, 2017), but the relationship among all three members remained unresolved (< 50% support) in our combined mt + nu analyses probably due to missing nuclear data for *M. taraiensis* (Figs. 1,



**Fig. 16.** The *Microhyla ornata* species group. **A.** Phylogenetic relationships depicted on a Maximum Likelihood phylogram based on mitochondrial 16S gene sequences from 104 samples representing three species. Accession numbers are cross-referenced in Table S1. Numbers above and below the branches indicate Bayesian Posterior Probabilities (BPP) and RAxML bootstrap values of > 50%, respectively. **B.** Geographical locations of the genetically and/or morphologically studied samples. **C.** Diagnostic morphological and acoustic characters for the group.

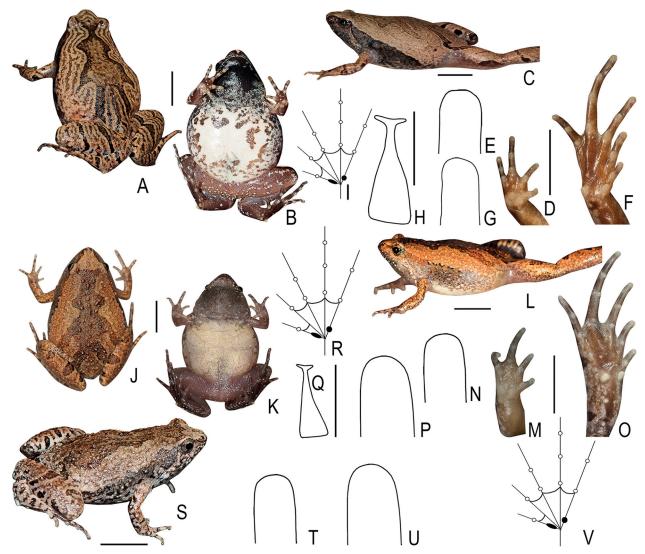


Fig. 17. Morphological characters of three members of the *Microhyla ornata* species group. A–I. *Microhyla nilphamariensis*. A. Dorsal view. B. Ventral view. C. Lateral view (A–C, in life, voucher SDBDU 2010.349). D. Ventral view of hand. E. Third finger tip. F. Ventral view of foot. G. Fourth toe tip. H. Terminal phalanx of fourth toe. I. Schematic illustration of webbing on foot (D–I, in preservation, voucher SDBDU 2010.350). J–R. *M. ornata*. J. Dorsal view. K. Ventral view. L. Lateral view (A–C, in life, voucher SDBDU 2016.3445). M. Ventral view of hand. N. Third finger tip. O. Ventral view of foot. P. Fourth toe tip. Q. Terminal phalanx of fourth toe. R. Schematic illustration of webbing on foot (D–I, in preservation, voucher SDBDU 2014.2555). S–V. *M. taraiensis*. S. Dorsolateral view (in life, not preserved). T. Third finger tip. U. Fourth toe tip. V. Schematic illustration of webbing on foot. Scale bars: 5 mm. (Photographs: S. D. Biju and S. Garg).

16). However, based on sequence divergence in the 16S gene, *M. nilphamariensis* was almost equally close to *M. taraiensis* (4.0-5.7%) as to *M. ornata* (3.8-5.5%), while *M. ornata* and *M. taraiensis* were more distantly related to each other (6.1-7.0%) (Table S2).

Acoustic comparison. The two recorded species in this group, *M. nilphamariensis* and *M. ornata*, can be differentiated from the other groups by their medium-sized pulsatile calls, 311.3–378.6 ms (311.3–368.7 ms in *M. nilphamariensis*; 321.1–378.6 ms in *M. ornata*). Further, *M. taraiensis* calls are known to have durations of 688–911 ms (KHATIWADA et. al., 2017). The calls of *M. nilphamariensis* and *M. ornata* differ from members of the *Microhyla rubra* group by slower pulse rate of 29.2–38.2

pulses/s (vs. faster, 73.8–83.3 pulses/s in *M. rubra*; and 65.8–70.5 pulses/s in *M. mihintalei*, as also shown previously by WIJAYATHILAKA *et al.*, 2016). The overall call structure of this group also has close resemblance with members of the *Microhyla fissipes* group. For differences with the *Microhyla achatina* group and *Microhyla fissipes* group, see their acoustic comparison sections (Fig. 18; Table S4).

**Note.** This group is widely distributed in India and neighboring regions of Bangladesh, Nepal, Sri Lanka, and possibly Bhutan and Pakistan.

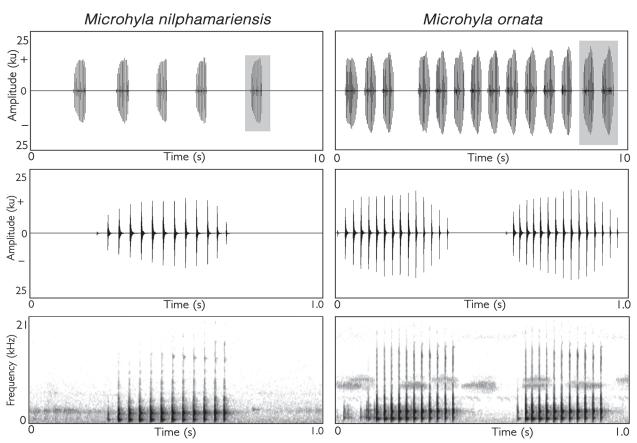


Fig. 18. Male advertisement calls of species in the *Microhyla ornata* group. Each species panel depicts (from top to bottom) oscillogram for ten-second call segment, oscillogram for 1-second call segment showing pulsatile structure, spectrogram for 1-second call segment.

# *Microhyla nilphamariensis* Howlader, Nair, Gopalan & Merilä, 2015

Nilphamari Narrow-mouthed Frog

(Figures 1-3, 16-18, S1, S2; Tables S1-S5; File S1)

**Original name and description.** *Microhyla nilphamariensis* Howlader M. S. A., Nair A., Gopalan S. V. & Merilä J. 2015. A new species of *Microhyla* (Anura: Microhylidae) from Nilphamari, Bangladesh, *PLoS One* 10(3): e0119825: 1–18. **Type.** Holotype MZH-2362, by original designation. **Type locality.** "from grass-field (25°48'06.12" N, 88°53'59.21" E), Koya Golahut, Saidpur, Nilphamari, Bangladesh". **Current status of specific name.** Valid name, as *Microhyla nilphamariensis* Howlader, Nair, Gopalan & Merilä, 2015.

**Description of holotype.** A detailed description of the holotype is available (HOWLADER *et al.*, 2015).

**Morphological comparison.** *Microhyla nilphamariensis* could be confused with *M. ornata* and *M. taraiensis* within the *Microhyla ornata* group. However, *M. nilphamariensis* differs from *M. ornata* and *M. taraiensis* by its lateral band, marking, or skin fold that starts from tip of the snout or nostril and approaches the groin on either side of the body, being more prominently blackishbrown and continuous (vs. less prominent); and ventral surfaces being mottled with various sized blackish-brown spots, more prominently on throat, chest, and margins of the belly (vs. throat grey to dark grey, chest and belly off-white, without prominent darker spots) (Fig. 16). Specifically, this species also differs from *M. ornata* by its upper eyelid width equal to internarial distance (vs. shorter); thigh nearly equal to shank length (vs. shorter) (Table S5); and inner metatarsal tubercle small and ovoid (vs. large and bean-shaped). Further, it differs from *M. taraiensis* by inner metatarsal tubercles being small and ovoid (vs. relatively smaller, rounded); and dorsum without prominent red spots (vs. dorsal surfaces including head with prominent and scattered red spots). For more difference with *M. taraiensis*, see discussion by HOWLADER *et al.* (2015).

**Genetic comparison.** Phylogenetically, *Microhyla nilphamariensis* is closely related to *M. ornata* and *M. taraiensis* (Figs. 1, 16). It differs from the two by uncorrected genetic distances of 3.8-5.5% and 4.0-5.7%, respectively, for the 16S gene (Table S2). Within *M. nilphamariensis*, intraspecific distances of up to 2.3% were observed, which was not surprising considering the wide distribution of this species across South Asia.

**Vocalization.** The calls of *Microhyla nilphamariensis* (SDBDU 2014.2482) were recorded at Amboli, by SDB and SG, on 19 July 2014, between 20:00–20:30 h, at air

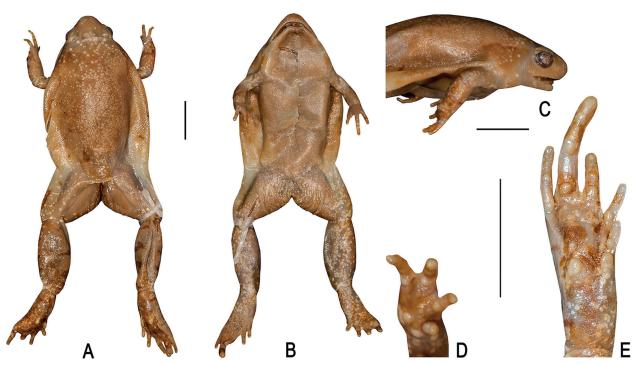


Fig. 19. Holotype of *Engystoma ornatum* (= *Microhyla ornata*), MNHNP 5035. A. Dorsal view. B. Ventral view. C. Lateral view of head. D. Ventral view of hand. E. Ventral view of foot. Scale bars: 5 mm.

temperature: 22.0°C dry bulb, 22.2°C wet bulb. The male produced a single type of call with pulsatile temporal structure. The calls were not delivered in groups and had uniform intervals. Calls had a mean duration of 337.2 ms (311.3-368.7 ms) with 11 pulses (10-12 pulses) delivered at a rate of 29.6 pulses/s (29.2-30.2 pulses/s), rise time of 240.6 ms (211.3-274.8 ms), and fall time of 82.8 ms (38.6-127.9 ms). The call spectrum was characterized by two broad peaks with mean dominant frequency of 2.3 kHz (Fig. 18; Table S4).

Acoustic comparison. The calls of *Microhyla nilpha-mariensis* differed from those of *M. ornata* by a relatively shorter rise time of 38.6–127.9 ms (vs. relatively longer, 112.2–164.4 ms) and slower pulse rate of 29.2–30.2 pulses/s (vs. faster, 34.9–38.2 pulses/s) (Fig. 18).

Distribution and natural history. Microhyla nilphamariensis is one of the most widely distributed Microhyla species of South Asia (Fig. 16) and is genetically confirmed to be present in Bangladesh (Dinajpur and Saidpur), India (Andhra Pradesh, Assam, Bihar, Chhattisgarh, Delhi, Karnataka, Kerala, Maharashtra, Odisha, Uttarakhand, and Uttar Pradesh), and Nepal (Mechi and Narayani) (Howlader et. al., 2015, Khatiwada et. al., 2017; GARG et al., 2018A). The previous study by GARG et al. (2018A) also discussed patterns of genetic differentiation among the various populations of this species. In the Western Ghats, this species is restricted to north of the Palghat Gap in Kerala up to Maharashtra. This species is found both in urban and forested areas throughout its range. Calling individuals were observed at Amboli (June-July) and Koyna (June-August) in Maharashtra state, and Madayipara (July) in Kerala state. Calling males were located close to temporary water bodies, either under grasses and low vegetation (Amboli and Koyna) or on laterite rock surfaces (Amboli and Madayipara).

**Notes.** This species could be confused or considered conspecific with two previously available names, *Engystoma malabaricum* Jerdon, 1853 and *Engystoma carnaticum* JERDON, 1853, currently under the synonymy of *Microhyla ornata*. For detailed discussion, see 'Notes' under *M. ornata*.

#### Microhyla ornata (Duméril & Bibron, 1841)

Ornate Narrow-mouthed Frog (ANANJEVA et al., 1988)

(Figures 1-3, 16-19, S1, S2; Tables S1-S5; File S1)

Original name and description. Engystoma ornatum Duméril A. M. C & Bibron G. 1841. Erpétologie Genérale ou Histoire Naturelle Complète des Reptiles, Volume 8, Paris: Librarie Enclyclopedique de Roret. Type. Holotype MNHNP 5035, according to Guibé (1950). Type locality. "côte Malabar", India. Current status of specific name. Valid name, as Microhyla ornata (Duméril & Bibron, 1841) (BOULENGER, 1882). Synonyms. Engystoma malabaricum Jerdon, 1853 and Engystoma carnaticum Jerdon, 1853 (BOULENGER, 1882).

**Comment.** A general description of the holotype is available (DUMÉRIL & BIBRON, 1841). This species was reported to occur widely in Asia (e.g., GÜNTHER, 1859 "1858"; STOLICZKA, 1870; BOULENGER, 1882; PARKER, 1934). Its

geographical range was restricted to South Asia after resolving taxonomic issues and misidentifications in literature (MATSUI *et al.*, 2005). The distribution was further clarified based on DNA barcoding and the species is currently known to occur only in Peninsular India and Sri Lanka (GARG *et al.*, 2018A). Since *M. ornata* has often been taxonomically confused with several morphologically similar species (e.g., *M. fissipes, M. okinavensis, M. mukhlesuri, M. mymensinghensis*, and *M. nilphamariensis*), below we provide a redescription of its holotype.

Redescription of Holotype MNHNP 5035 (measurements in mm) (Fig. 19). A small-sized (SVL 22.9), slender adult male; head small (HW 6.4, HL 5.1), wider than long (HW/HL ratio 1.3); snout subovoid in dorsal and ventral view, rounded in lateral view, protruding, its length (SL 2.7) longer than horizontal diameter of eye (EL 1.9); loreal region obtuse with rounded canthus rostralis; interorbital space wider (IUE 2.4) than upper eyelid width (UEW 1.2); nostril oval without lateral flap of skin, closer to tip of snout (NS 0.8) than eye (EN 1.3); tympanum not visible externally, faintly developed supratympanic fold extending from posterior corner of upper eyelid to shoulder; eye diameter (EL 1.9); vomerine teeth absent; tongue small, oval, without papillae. Arms short, forearm length (FAL 3.7) shorter than the hand (HAL 4.9); relative length of fingers I  $\leq$  II  $\leq$  IV  $\leq$  III (FL<sub>1</sub> 1.1,  $FL_{II}$  1.6,  $FL_{III}$  3.2,  $FL_{IV}$  1.7); tips of all fingers without discs and grooves; dermal fringe on fingers absent, webbing between fingers absent; subarticular tubercles rather prominent; three palmar tubercles, well-developed, oval; supernumerary tubercles absent; nuptial pad absent. Hind limbs short, thigh (THL 9.7) shorter than shank (SHL 10.1) and foot (FOL 9.9); distance from base of tarsus to tip of toe IV (TFOL 14.3); relative length of toes I<II<V<III<IV; toe tips without discs and grooves, toes without dermal fringes, terminal phalanges of toes T-shaped, webbing between toes rudimentary: I2  $^{+}-2^{2}/_{3}II2-3^{+}III3^{+}-4^{+}IV4^{+}-3V$ ; subarticular tubercles prominent, all present, circular; inner metatarsal tubercle prominent (IMT 0.9), oval; outer metatarsal slightly smaller than inner tubercle (OMT 0.7), prominent; supernumerary tubercles absent.

Skin of snout, between eyes, sides of head smooth to shagreened; anterior and posterior part of back, and upper and lower part of flanks sparsely granular; dorsal parts of forelimb, thigh, tibia, and tarsus smooth to shagreened; posterior part of thighs and cloacal region coarsely granular; and ventral surface smooth (Fig. 19).

**Morphological comparison.** *Microhyla ornata* could be confused with *M. nilphamariensis* and *M. taraiensis* within the *Microhyla ornata* group (Fig. 16). However, *M. ornata* differs from *M. taraiensis* by its elongate or bean-shaped metatarsal tubercle (vs. rounded), rounded outer metatarsal tubercle (vs. elongate), and dorsum without prominent red spots (vs. dorsal surfaces including the head with prominent and scattered red spots). For more differences with *M. taraiensis*, see discussion by

HOWLADER *et al.* (2015). For detailed comparison with *M. nilphamariensis*, see the morphological comparison section of that species.

**Genetic comparison.** Phylogenetically, *Microhyla ornata* is closely related to *M. nilphamariensis* and *M. taraiensis* (Figs. 1, 16). It differs from the two by uncorrected genetic distances of 3.8-5.5% and 6.1-7.0%, respectively, for the 16S gene (Table S2). The Indian and Sri Lankan populations of *M. ornata* are genetically similar (0.2-0.6%).

**Vocalization.** The calls of *Microhyla ornata* (SDBDU 2014.2794) were recorded at Coimbatore, by SDB and SG, on 8 October 2014, between 21:00-22:00 h, at air temperature:  $28.5^{\circ}$ C dry bulb,  $26.5^{\circ}$ C wet bulb. The male produced a single type of call with pulsatile temporal structure. The calls were not delivered in groups and had uniform intervals. Calls had a mean duration of 333.8 ms (321.1-378.6 ms) with 13 pulses (13-14 pulses) delivered at a rate of 37.3 pulses/s (34.9-38.2 pulses/s), rise time of 193.4 ms (152.6-215.3 ms), and fall time of 129.8 ms (112.2-164.4 ms). The call spectrum was characterized by two broad peaks with mean dominant frequency of 2.6 kHz (Fig. 18; Table S4).

Acoustic comparison. The calls of *Microhyla ornata* have an overall structural resemblance with *M. nilpha-mariensis* (Fig. 18). For differences, see the acoustic comparison section of that species.

Distribution and natural history. Microhyla ornata was believed to be a widely distributed species throughout South Asia (MATSUI et al., 2011), however its distribution was recently restricted to Peninsular India and Sri Lanka (GARG et al., 2018A). Based on genetically confirmed records, currently, in India Mornata is known to occur in the states of Andhra Pradesh, Karnataka, Kerala, and Tamil Nadu. The present study also genetically confirms the records of *M. ornata* from Sri Lanka (Fig. 16; Table S1). This species is predominantly found outside forest areas, mostly in agricultural fields or under wayside vegetation close to permanent or temporary water bodies in urban landscapes. Breeding activities were usually observed during the early monsoon season (June-July), although animals can often be heard calling throughout the monsoon, immediately after rains. This species is often sympatric with members of the Microhyla rubra group and/ or Microhyla zeylanica group.

**Notes.** Engystoma malabaricum Jerdon, 1853 is currently placed under the synonymy of *Microhyla ornata* (BOU-LENGER, 1882). Some of the characters mentioned in the original description of this taxon (such as "Isabella color above, varied with dark angular markings, sides dark purplish, throat ditto, limbs barred") are usually more prominent and considered diagnostic for two other species from this region, i.e., *Microhyla nilphamariensis* and *M. sholigari*. Further, the sount-vent size of Engystoma malabaricum is stated as "Length 1  $1/10^{\text{th}}$ " (= SVL 27.9 mm), which is closer to the size range of *Microhyla* nilphamariensis (SVL 19–24 mm) than *M. sholigari* (SVL 16–18 mm). Hence, *M. nilphamariensis* could be conspecific with *Engystoma* malabaricum Jerdon, 1853. However, the original name bearing type of *Engystoma* malabaricum is untraceable and likely to be lost (JERDON, 1870).

Another nomen, Engystoma carnaticum Jerdon, 1853, is also currently under the synonymy of Microhyla ornata (BOULENGER, 1882). Although the type specimen of this taxon is also considered lost (JERDON, 1870), two specimens available at ZSIC (ZSIC 3582, female, SVL 25 mm; ZSIC 3583, male, SVL 18.5 mm) and identified as Diplopelma carnaticum Stoliczka, 1870 (= Engystoma carnaticum Jerdon, 1853) by STOLICZKA (1870) are comparable with Microhyla nilphamariensis in sountvent size, "three quarters of an inch" (= SVL 19.05 mm) and "largest specimens (somewhat exceeding one inch in length of body)" (= SVL > 25.4 mm), and the overall dorsal and ventral coloration. This taxon was originally described from "the Carnatic", South India with size stated as "Length 9/10th of an inch" (= SVL 22.86 mm) (Jerdon, 1853). Subsequently, this species was also reported to be widely distributed, "occurs all through Barma and Bengal, probably extending into the eastern Panjab, and southward through the Central Provinces and Orissa into the Carnatic" (STOLICZKA, 1870), more or less matching the distribution range of M. nilphamariensis (GARG et al., 2018A). However, the specimens of Diplopelma carnaticum available at ZSIC are found to be in a poorly preserved or damaged condition and their type status also remains unclear.

## *Microhyla taraiensis* Khatiwada, Shu, Wang, Thapa, Wang & Jiang, 2017

Tarai Narrow-mouthed Frog (Khatiwada, Shu, Wang, Thapa, Wang & Jiang, 2017)

(Figures 1-3, 16, 17, S1, S2; Tables S1-S5; File S1)

**Original name and description.** *Microhyla taraiensis* Khatiwada J. R., Shu G. C., Wang S. H., Thapa A., Wang B. & Jiang J. 2017. A new species of the genus *Microhyla* (Anura: Microhylidae) from Eastern Nepal, *Zootaxa* 4254 (2): 221–239. **Type.** Holotype NHM-TU-17A-0110, by original designation. **Type locality.** "Jamun Khadi, Jhapa district, Nepal, 26.65358°N & 87.91161°E; elevation 119 m asl". **Current status of specific name.** Valid name, as *Microhyla taraiensis* Khatiwada, Shu, Wang, Thapa, Wang & Jiang, 2017.

**Description of holotype.** A detailed description of the holotype is available (KHATIWADA *et al.*, 2017).

**Morphological comparison.** *Microhyla taraiensis* could be confused with *M. ornata* and *M. nilphamariensis* within the *Microhyla ornata* group. However, it differs from the two by relatively larger adult size, dorsum with

prominent red spots, and smaller inner metatarsal tubercles. For more differences with *M. nilphamariensis* and *M. ornata* see their morphological comparison sections and the original description (KHATIWADA *et al.*, 2017).

**Genetic comparison.** Phylogenetically, *Microhyla taraiensis* is closely related to *M. nilphamariensis* and *M. ornata* (Figs. 1, 16). It differs from the two by uncorrected genetic distances of 4.0-5.7% and 6.1-7.0%, respectively, for the 16S gene (Table S2).

**Distribution and natural history.** *Microhyla taraiensis* is currently known only from its type locality Jamun Khadi in Eastern Nepal. Although we did not survey Indian regions neighboring Nepal, this species is likely to be present in adjoining low elevation areas of Bihar and West Bengal. The original description reported this species only from rice fields surrounding a wetland area, where it is found to occur sympatrically with *M. nilphamariensis* (KHATIWADA *et al.*, 2017).

#### Microhyla rubra species group

(Figures 1-3, 20-23, S1, S2; Tables S1-S5; File S1)

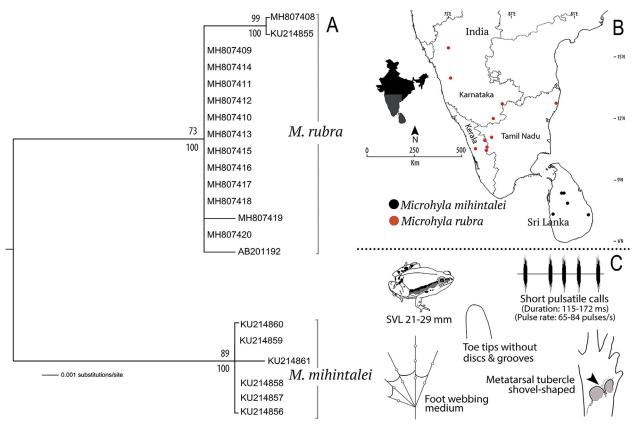
**Members included.** South Asia — *Microhyla mihintalei* and *M. rubra*.

**Diagnosis.** This group is unique among all the other *Microhyla* groups of South Asia and can be distinguished by two major characters, terminal phalanges of toes simple with rounded tips and large shovel-shaped metatarsal tubercles on foot (Fig. 20).

**Morphological comparison.** For comparison with the *Microhyla achatina* group, *Microhyla berdmorei* group, *Microhyla fissipes* group, and *Microhyla ornata* group, see morphological comparison sections of the respective groups. The *Microhyla rubra* group differs from *Microhyla zeylanica* group by its finger and toe tips rounded without grooves (vs. toe tips having small discs with circum-marginal grooves in *M. zeylanica*, or with prominent dorso-terminal grooves and cover bifurcate distally in all other species), terminal phalanges of toes simple with rounded tips (vs. T-shaped), and well-developed shovel-shaped inner and outer metatarsal tubercles (vs. weakly-developed, not shovel-shaped) (Fig. 21).

Genetic relationships. Phylogenetically, the *Microhyla rubra* group can be characterized as the most inclusive clade containing *Microhyla mihintalei* and *M. rubra*, but none of the other clades that have been genetically studied so far within the entire radiation of *Microhyla*. The sister relationship between *M. mihintalei* and *M. rubra* is well supported, and together these two members are closely allied to the *Microhyla ornata* group (Figs. 1, 20).

Acoustic comparison. The two species in this group, Microhyla mihintalei and M. rubra, can be differenti-



**Fig. 20.** The *Microhyla rubra* species group. **A.** Phylogenetic relationships depicted on a Maximum Likelihood phylogram based on mitochondrial 16S gene sequences from 27 samples representing two species. Accession numbers are cross-referenced in Table S1. Numbers above and below the branches indicate Bayesian Posterior Probabilities (BPP) and RAxML bootstrap values of > 50%, respectively. **B.** Geographical locations of the genetically and/or morphologically studied samples. **C.** Diagnostic morphological and acoustic characters for the group.

ated from the other groups by their short pulsatile calls, 115.3-171.7 ms (158.5-171.7 ms in *M. mihintalei*, and 115.3-142.4 ms in *M. rubra*) (Fig. 22). For comparison with the *Microhyla achatina* group, *Microhyla fissipes* group, and *Microhyla ornata* group, see the acoustic sections of the respective groups.

**Note.** This group is restricted to Peninsular India and Sri Lanka (WIJAYATHILAKA *et al.*, 2016). Records outside this region, specifically from western Myanmar (WOGAN *et al.*, 2008) and Nepal (ANDERS, 2002), are doubtful.

#### *Microhyla mihintalei* Wijayathilaka, Garg, Senevirathne, Karunarathna, Biju & Meegaskumbura, 2016

Mihintale Red Narrow-mouthed Frog (WIJAYATHILAKA et al., 2016)

(Figures 1-3, 20-22, S1, S2; Tables S1-S5; File S1)

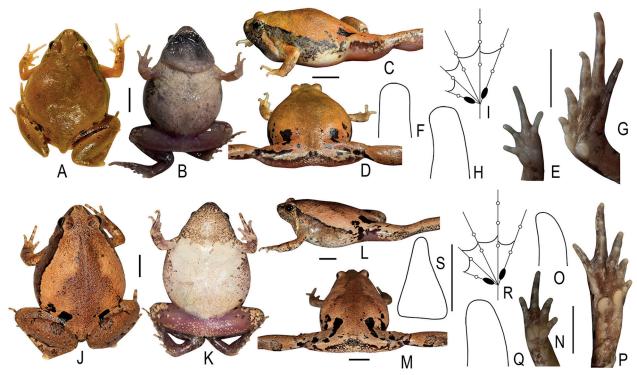
**Original name and description.** *Microhyla mihintalei* Wijayathilaka N., Garg S., Senevirathne G., Karunarathna N., Biju S. D. & Meegaskumbura M. 2016. A new species of *Microhyla* (Anura: Microhylidae) from Sri Lanka: an integrative taxonomic approach, *Zootaxa* 4066: 331–342. **Type.** Holotype DZ 1553, by

original designation. **Type locality.** "Anuradhapura (8.3541°N, 80.3967°E, 90 m a.s.l) Sri Lanka". **Current status of specific name.** Valid name, as *Microhyla mihintalei* Wijayathilaka, Garg, Senevirathne, Karunarathna, Biju & Meegaskumbura, 2016.

**Description of holotype.** A detailed description of the holotype is available (WIJAYATHILAKA *et al.*, 2016).

**Morphological comparison.** *Microhyla mihintalei* could be confused with *M. rubra*, the only other member of the *Microhyla rubra* group. However, *M. mihintalei* differs from *M. rubra* by its relatively smaller adult male size, SVL 21–28 mm (vs. relatively larger, male SVL 24–30 mm), thigh nearly equal to shank and foot length, male, THL 10.8–12.5 mm, SHL 10.9–12.7 mm, FOL 10.8–12.2 mm, N=9 (vs. longer, male, THL 12.0–14.3 mm, SHL 11.9–12.4 mm, FOL 11.5–13.1 mm, N=8), and dorsal skin shagreened to sparsely granular (vs. granular) (Figs. 20, 21).

**Genetic comparison.** *Microhyla mihintalei* is the sister species of *M. rubra* (Figs. 1, 20) and differs from it by uncorrected genetic distances of 2.5-3.2% based on the 16S gene (Table S2).



**Fig. 21.** Morphological characters of two members of the *Microhyla rubra* species group. **A–I.** *Microhyla mihintalei*. **A.** Dorsal view. **B.** Ventral view. **C.** Lateral view. **D.** Posterior view of thighs (A–D, in life, voucher DZ 1553). **E.** Ventral view of hand. **F.** Third finger tip. **G.** Ventral view of foot. **H.** Fourth toe tip. **I.** Schematic illustration of webbing on foot (E–I, in preservation, voucher DZ 1557). **J–S.** *M. rubra*. **J.** Dorsal view. **K.** Ventral view. **L.** Lateral view. **M.** Posterior view of thighs (J–M, in life, voucher SDBDU 2014.2539). **N.** Ventral view of hand. **O.** Third finger tip. **P.** Ventral view of foot. **Q.** Fourth toe tip. **R.** Schematic illustration of webbing on foot. **S.** Terminal phalanx of fourth toe (L–Q, in preservation, voucher SDBDU 2014.2792). Scale bars: 5 mm. (Photographs: S. D. Biju and S. Garg).

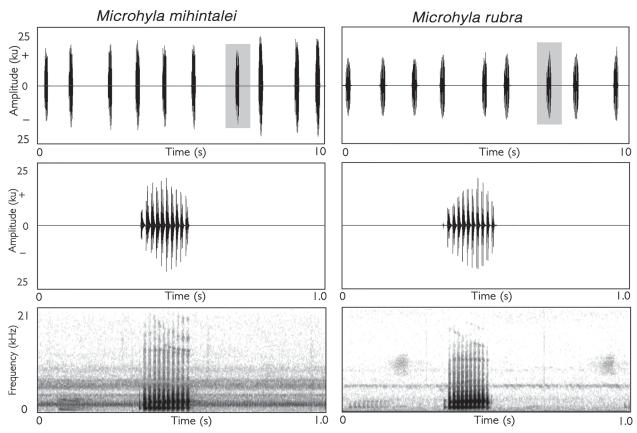


Fig. 22. Male advertisement calls of species in the *Microhyla rubra* group. Each species panel depicts (from top to bottom) oscillogram for ten-second call segment, oscillogram for 1-second call segment showing pulsatile structure, and spectrogram for 1-second call segment.

**Vocalization.** The calls of *Microhyla mihintalei* (DZ 1445) were recorded at Mihintale, Sri Lanka, by MM and team on 27 September 2014, between 19:30-20:00 h, at air temperature: 27°C dry bulb, 25.5°C wet bulb. The males produce a single type of call with pulsatile temporal structure (WIJAYATHILAKA *et al.*, 2016). The calls are not delivered in groups, had short mean duration of 162.6 ms (158.5-171.7 ms), with 12 pulses (11-12 pulses) delivered at a rate of 68.4 pulses/s (65.8-70.5 pulses/s), call rise time of 76.8 ms (66.2-84.3 ms), and call fall time of 79.2 ms (60.1-105.1 ms). The call spectrum was characterized by a single broad peak with mean dominant frequency of 2.3 kHz (Fig. 22; Table S4).

Acoustic comparison. The calls of *Microhyla mihintalei* differed from those of *M. rubra* by a relatively longer duration 158.5–171.7 ms (vs. shorter, 115.3–142.4 ms) and slower pulse rate of 65.8–70.5 pulses/s (vs. 73.8–83.3 pulses/s) (Fig. 22).

**Distribution and natural history.** *Microhyla mihintalei* is endemic to Sri Lanka where it is widely distributed in the lowland dry zone. This species is often associated with stagnant water bodies and banks of slow flowing streams. It is also known to burrow or hide in crevices during daytime. So far, the presence of this species has been genetically confirmed at Anuradhapura, Maakandura, Ampara, Mihintale, and Dambulla (WIJAYATHILAKA et al., 2016), but it is believed to occur more widely in dry lowlands of the island (Fig. 20). This species can be found sympatrically with *M. ornata* and the tadpoles of both species have been observed in same water bodies (WIJAYATHILAKA et al., 2016).

#### Microhyla rubra (Jerdon, 1854 "1853")

Red Narrow-mouthed Frog (DAS & DUTTA, 1998)

(Figures 1-3, 20-23, S1, S2; Tables S1-S5; File S1)

**Original name and description.** *Engystoma rubrum* Jerdon T. C. 1854 "1853". Catalogue of reptiles inhabiting the Peninsula of India, *Journal of the Asiatic Society of Bengal* 22: 522–534. **Neotype.** By present designation, ZSI/WGRC/V/A/960, an adult male, SVL 27.9 mm, collected by SD Biju and Sonali Garg on 25 July 2014. **Neotype locality.** Bannerghatta, Karnataka, India. **Current status of specific name.** Valid name, as *Microhyla rubra* (Jerdon, 1854 "1853").

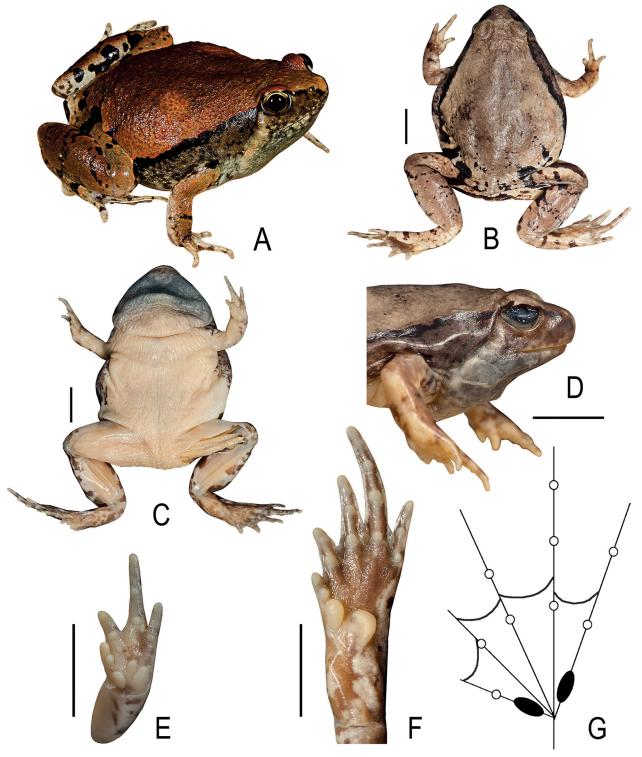
**Designation of neotype.** This species was described from the "Carnatic near rivers, in sandy banks" and "also Ceylon" without mention of any specimens. The original name bearing type for this taxon was presumed to be at ZSIC but considered lost (JERDON, 1870). Thereafter, this species was known only from its original description (DUTTA & MANAMENDRA-ARACHCHI, 1996). Since, the original description states distant localities in two different countries, India and Sri Lanka, the origin of the type

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specimen that JERDON (1854 "1853") used for describing this nominal taxon is unclear. The populations identified as Microhyla rubra from Sri Lanka are currently assigned to another species, M. mihintalei (WIJAYATHILAKA et al., 2016). A collection from Bannerghatta (ZSI/WGRC/ V/A/960), which is part of the "Carnatic" (type locality stated in India), is comparable with the original description of Engystoma rubrum Jerdon, 1854 "1853" by its snout-vent size 27.9 mm ("Length 1 1/10th inch"=27.94 mm), dorsal color brick red ("Indian red above"), and thigh markings dark brownish-black ("some black marks on the legs"). In order to avoid confusion concerning the identity of Microhyla rubra, especially with its closely related congener M. mihintalei, as well as to define this taxon objectively and establish taxonomic stability, in accordance with Article 75 of The Code we find it necessary to designate a neotype for Engystoma rubrum Jerdon, 1854 "1853". Here, we formally designate, ZSI/WGRC/ V/A/960, an adult male from Bannerghatta, Karnataka, as the neotype of Engystoma rubrum Jerdon, 1853. The neotype description provided below also shows that the neotype is largely consistent with what is known of the former name-bearing type.

Description of neotype (measurements in mm) (Fig. 23). A large-sized (SVL 27.9), robust adult male; head small (HW 8.1, HL 6.7, IFE 4.2, IBE 7.8), wider than long (HW/HL ratio 1.3); snout subovoid in dorsal and ventral view, rounded in lateral view, protruding, its length (SL 3.6) longer than horizontal diameter of eye (EL 2.6); loreal region obtuse with rounded canthus rostralis; interorbital space wider (IUE 2.7) than upper eyelid width (UEW 2.1); nostril oval without lateral flap of skin, closer to tip of snout (NS 1.2) than eye (EN 1.6); tympanum not visible externally, faintly developed supratympanic fold extending from posterior corner of eye to shoulder; eye diameter (EL 2.6); vomerine teeth absent; tongue small, oval, without papillae. Arms short, forearm length (FAL 5.2) shorter than the hand (HAL 6.9); relative length of fingers I< II< IV< III (FL<sub>1</sub> 0.9,  $FL_{II}$  1.6,  $FL_{III}$  3.9,  $FL_{IV}$  1.7); tips of all fingers without discs and grooves; dermal fringe on fingers weaklydeveloped, webbing absent between fingers; subarticular tubercles rather prominent; three palmar tubercles, well-developed, oval; supernumerary tubercles absent; nuptial pad absent. Hind limbs short, thigh (THL 14.3) longer than shank (SHL 12.1) and foot (FOL 12.8); distance from base of tarsus to tip of toe IV (TFOL 17.5); relative length of toes I< II< V< III< IV; toe tips without discs and grooves, toes with dermal fringes, terminal phalanges of toes simple with rounded tips, webbing between toes present, small:  $I1 - 2^{-1}I1^{+} - 2^{1}/_{2}III2^{1}/_{2} - 3^{1}/_{2}IV$  $4^{-}-2^{1}/_{2}V$ ; subarticular tubercles prominent, all present, circular; inner metatarsal tubercle prominent (IMT 1.4), oval, shovel-shaped; outer metatarsal tubercle (OMT 1.6) slightly larger than the inner, shovel-shaped; supernumerary tubercles absent.

Skin of snout, between eyes, sides of head smooth to shagreened; anterior and posterior parts of back, and



**Fig. 23.** Neotype of *Microhyla rubra* (ZSI/WGRC/V/A/960). **A.** Dorsolateral view (in life). **B.** Dorsal view. **C.** Ventral view. **D.** Lateral view of head. **E.** Ventral view of hand. **F.** Ventral view of foot. **G.** Schematic illustration of webbing on foot (B–G, in preservation). Scale bars: 5 mm. (Photographs: S. D. Biju).

upper and lower parts of flank granular; dorsal parts of forelimb, thigh, tibia, and tarsus smooth to shagreened; posterior parts of thigh and cloacal region coarsely granular; ventral surfaces smooth (Fig. 23).

Neotype color in preservation (Fig. 23). Dorsum dark grey; a faint light greyish-brown lateral band extending

from posterior corner of the eye to the groin, margin towards the dorsum dark greyish-brown; lateral surfaces of head and tympanic area dark grey; dorsal surfaces of limbs grey with discontinuous dark greyish-brown crossbands; groin light grey with dark greyish-brown patches; posterior parts of back with scattered dark greyish-brown spots; thighs with a pair of prominent dark greyishbrown markings that extend towards the posterior end of dorsum and groin; a light brown crescent-shaped marking above the cloacal opening; ventral surface light grey, throat with dark grey calling patch.

Neotype color in life (Fig. 23). Dorsum light reddishbrown with a dark brown median band extending from the upper eyelids to the vent; a distinct blackish-brown lateral band extending from posterior corner of the eye to the groin, margin towards the dorsum darker blackishbrown; lateral surfaces of head and tympanic area dark grey with black spots; groin creamy-white with black patches; limbs light reddish-brown with discontinuous dark brown cross-bands; posterior parts of thigh and tibia light brown with irregular black markings; thighs with a pair of prominent black markings that extend towards the posterior end of dorsum and groin; a narrow black streak extending from the cloacal opening towards the knee on either side; ventral surface creamy-white, throat with dark blackish-brown calling patch.

**Morphological variations.** For morphometric data from eight adult males including the neotype, see Table S5. SDBDU 2014.2558: dorsum with irregular black spots, more prominent towards the center; SDBDU 2014.2560: prominently granular dorsum; SDBDU 2014.2560: dorsum sparsely granular with a light brownish-grey median band; SDBDU 2014.2543: dorsum with a wider median band and small golden yellow spot behind the left eye.

**Secondary sexual character.** Males with a single vocal sac externally visible on the lower jaw.

**Morphological comparison.** *Microhyla rubra* could be confused with *M. mihintalei*. For comparison with *M. mihintalei* see the morphological comparison section of that species.

**Genetic comparison.** Phylogenetically, *Microhyla rubra* is the sister species of *M. mihintalei* (Figs. 1, 20) and differs from it by uncorrected genetic distances of 2.5-3.2% based on the 16S gene (Table S2).

**Vocalization.** The calls of *Microhyla rubra* (SDBDU 2014.2791) were recorded at Coimbatore, by SDB and SG, on 8 October 2014, between 21:00-21:30 h, at air temperature: 28.5°C dry bulb, 26.5°C wet bulb. The male produced a single type of call with pulsatile temporal structure. The calls were not delivered in groups and had uniform intervals. Calls had a mean duration of 130.6 ms (115.3–142.4 ms) with 11 pulses (10–12 pulses) delivered at a rate of 80.4 pulses/s (73.8–83.3 pulses/s), rise time of 69.8 ms (35.1–90.3 ms), and fall time of 60.8 ms (39.1–80.3 ms). The call spectrum was characterized by a single broad peak with mean dominant frequency of 2.2 kHz (Fig. 22; Table S4).

Acoustic comparison. The calls of *Microhyla rubra* were similar to those of *M. mihintalei* in most of the stud-

ied temporal and spectral properties. They differed from those of *M. mihintalei* by relatively shorter duration of 115.3–142.4 ms (vs. longer, 158.5–171.7 ms) and faster pulse rate of 73.8–83.3 pulses/s (vs. slower, 65.8–70.5 pulses/s) (Fig. 22).

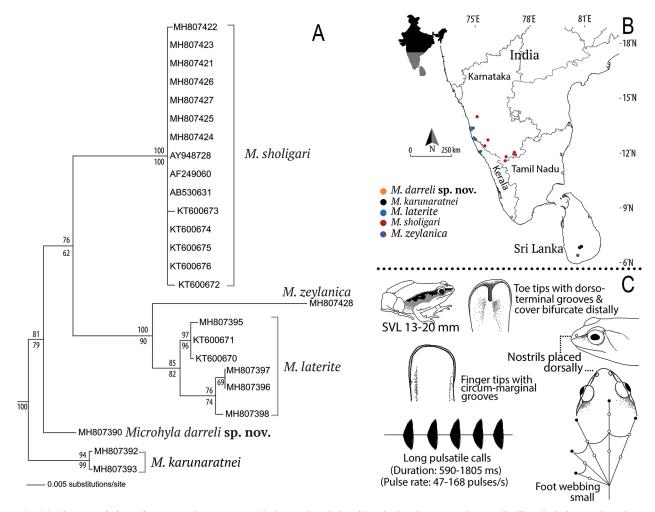
Distribution and natural history. Microhyla rubra is reported widely in India but the present study genetically confirmed its occurrence only in the states of Karnataka, Kerala, and Tamil Nadu. The reports of this species from Assam, Mizoram, and Nagaland (MATHEW & SEN, 2010) are doubtful. Based on the accompanying image (MATHEW & SEN, 2010: page 68), the reported specimen does not show any of the diagnostic characters of M. rubra and could be a misidentification of other Microhyla species (M. nilphamariensis, M. mukhlesuri, or possibly M. mymensinghensis) found in those regions. Outside India, this species was previously reported from western Myanmar (WOGAN, 2008) and Nepal (ANDERS, 2002), however these are also considered doubtful and likely to be misidentifications. In our study, this species was found close to permanent or temporary water bodies in secondary forest patches (Kerala: Parambikulam), agricultural land close to forests (Karnataka: Bannerghatta, BR hills, and Shimoga), rural settlements (Kerala: Mannuthy, Tamil Nadu: Perumalkovilpetty and Meenakshipuram), and urban areas (Tamil Nadu: Coimbatore). Calling males were recorded from edges of a seasonal pond at Coimbatore (18:00-23:00 h) during the month of October. This species occurs sympatrically with members of the Microhyla ornata group (Bannerghatta and Coimbatore) or both the Microhyla ornata and Microhyla zeylanica groups (BR Hills and Shimoga).

#### Microhyla zeylanica species group

(Figures 1-3, 24-29, S1, S2; Tables S1-S5; Files S1, S2)

**Members included.** South Asia — *Microhyla darreli* **sp. nov.**, *M. karunaratnei*, *M. laterite*, *M. sholigari*, and *M. zeylanica*.

Diagnosis. This group is distinguished from other Microhyla groups of South Asia by the following suite of characters: small-sized adults (male SVL 13-20 mm, female SVL 15-23 mm); dorsal skin smooth to shagreened; nostrils placed towards the dorsal side of the snout (Fig. 24); toe discs with circum-marginal grooves (in *M. zeylanica*), or prominent dorso-terminal grooves and cover bifurcate distally (in all other species); elongate inner metatarsal tubercle, small and rounded outer metatarsal tubercle; small webbing between toes, not extending beyond the second subarticular tubercle on either side of toe IV; presence of a narrow mid-dorsal skin fold or line extending from tip of the snout to the vent; presence of a prominent lateral band, marking, or skin fold starting from tip of the snout or nostril and approaching the groin on either side of the body (Fig. 24).



**Fig. 24.** The *Microhyla zeylanica* species group. **A.** Phylogenetic relationships depicted on a Maximum Likelihood phylogram based on mitochondrial 16S gene sequences from 25 samples representing four known and one new species. Accession numbers are cross-referenced in Table S1. Numbers above and below the branches indicate Bayesian Posterior Probabilities (BPP) and RAxML bootstrap values of > 50%, respectively. **B.** Geographical locations of the genetically and/or morphologically studied samples. **C.** Diagnostic morphological and acoustic characters for the group.

Morphological comparison. Species in this group differ from members of the Microhyla achatina group by nostrils placed towards the dorsal side of the snout (vs. towards the lateral side), and specifically from the South Asian members by small webbing between toes, extending up to the second subarticular tubercle on either side of toe IV (vs. rudimentary in *M. kodial*); from the *Mi*crohyla berdmorei group by relatively smaller adult size, male SVL 13-20 mm, female SVL 15-23 mm (vs. larger, male SVL 33-36 mm), terminal phalanges of toes Tshaped (vs. Y-shaped), and small webbing between toes, not extending beyond the second subarticular tubercle on either side of toe IV (vs. large webbing, beyond the first subarticular tubercle on either side of toe IV); from the Microhyla fissipes group by relatively smaller adult size, male SVL 13-20 mm, female SVL 15-23 mm (vs. larger, male SVL 17-25 mm, female SVL 22-28 mm), nostrils placed towards the dorsal side of the snout (vs. towards the lateral side), toe discs with circum-marginal grooves in M. zeylanica or prominent dorso-terminal grooves and cover bifurcate distally in all other species

(vs. rounded or having small discs without grooves), and small webbing between toes (vs. absent or rudimentary); from the Microhyla ornata group by relatively smaller adult size, SVL 13-20 mm, female SVL 15-23 mm (vs. larger, male SVL 15–24 mm, female SVL 22–28 mm), nostrils placed towards the dorsal side of the snout (vs. towards the lateral side), and toe discs with circum-marginal grooves in M. zeylanica or prominent dorso-terminal grooves and cover bifurcate distally in all other species (vs. toe discs without grooves); from the Microhyla rubra group by relatively smaller adult size, SVL 13-20 mm, female SVL 15-23 mm (vs. larger, male SVL 21-30 mm, female SVL 23-31 mm), terminal phalanges of toes T-shaped (vs. simple with rounded tips), toe discs with circum-marginal grooves in M. zeylanica or prominent dorso-terminal grooves and cover bifurcate distally in all other species (vs. toe discs without grooves), and inner and outer metatarsal tubercles relatively weak and not shovel-shaped (vs. well-developed and shovel-shaped) (Fig. 24). For more differences, see the morphological comparison sections of the respective groups.

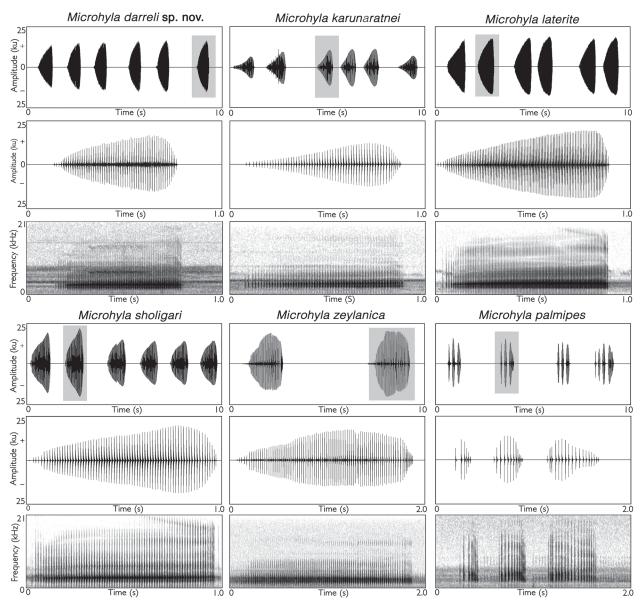


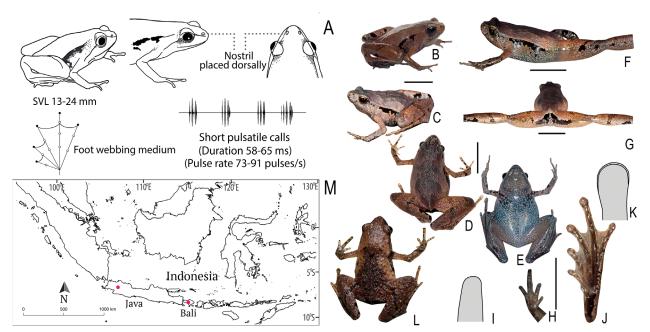
Fig. 25. Male advertisement calls of five South Asian species in the *Microhyla zeylanica* group (*Microhyla darreli* sp. nov., *M. karunarat-nei*, *M. laterite*, *M. sholigari*, and *M. zeylanica*) and an acoustically related Southeast Asian species (*Microhyla palmipes*). Each species panel depicts (from top to bottom) oscillogram for ten-second call segment, oscillogram for 1-second call segment showing pulsatile structure, and spectrogram for 1-second call segment.

**Genetic relationships.** Phylogenetically, *Microhyla zeylanica* group can be characterized as the most inclusive clade (Peninsular India + Sri Lankan radiation) containing *Microhyla darreli* **sp. nov.**, *M. karunaratnei*, *M. laterite*, *M. sholigari*, and *M. zeylanica*, but none of the other clades that have been genetically studied so far within the entire radiation of *Microhyla* (Fig. 1).

In our study, the grouping of members in the *Micro-hyla zeylanica* group is based on close relationship of two previously unassigned and poorly known species, *M. karunaratnei* and *M. zeylanica*, with *M. laterite*, *M. sholigari*, and the new species *Microhyla darreli* **sp. nov.** (Figs. 1, 24), although relationships among these five species were either conflicting or remained unresolved in the separate mt and combined mt + nu analyses. Based on 16S genetic distances, the new species *M. dar-*

*reli* **sp. nov.** was closest to *M. karunaratnei* (2.5%) and *M. sholigari* (3.1–3.3%), but shared a haplotype (for the nu gene) with *M. laterite* (Fig. 2), from which it differed by 3.8-4.2%, instead of the former two (Table S2). Among all, *M. zeylanica* was the most distinct species with closest genetic relation to *M. laterite* (3.8–4.6%) and > 5% divergence from other members of the group (Table S2). For detailed discussion on intra- and interspecific pairwise divergence see the respective species accounts.

Acoustic comparison. Species in this group can be differentiated from the other groups by their considerably longer calls, 600-1800 ms (vs. shorter in all other groups) (Fig. 25; Table S4). For differences, see the acoustic comparison sections of the respective groups.



**Fig. 26.** *Microhyla palmipes.* **A.** Key morphological and acoustic characters. **B.** Dorsolateral view (not preserved). **C.** Dorsolateral view (not preserved). **D.** Dorsal view. **E.** Ventral view. **F.** Lateral view. **G.** Posterior view of thighs (D–G, in life, voucher UIMZ 0142). **H.** Ventral view of hand. **I.** Third finger tip. **J.** Ventral view of foot. **K.** Fourth toe tip (H–K, in preservation, voucher UIMZ 0142). **L.** Dorsal view (not preserved). Scale bars: 5 mm. (Photographs: S. D. Biju; C & L, F. Alhadi).

**Distribution.** This group is endemic to Peninsular India and Sri Lanka.

Note. Another small-sized species, Microhyla palmipes (SVL 12-16 mm, N=8) from Southeast Asia (Java, Indonesia) shows certain degree of morphological similarity with members of the Microhyla zeylanica group, particularly with the Sri Lankan species M. zeylanica due to characters such as the placement of nostrils towards the dorsal side of the snout, presence of circum-marginal grooves on the toe discs, and presence of a narrow middorsal skin fold or line extending from tip of the snout to the vent (Fig. 26). However, the calls of M. palmipes are distinct and unlike members of the Microhyla zevlanica group or any other studied South Asian Microhyla groups. The calls of M. palmipes are very short in duration (mean 109.6 ms) and delivered in groups of 3-4calls (Fig. 25; File S2). Further studies based on robust phylogenies combined with morphological and acoustic evidence could provide more insights on the systematic relationship of M. palmipes with member of the Microhyla zeylanica group.

#### Microhyla darreli sp. nov.

ZOOBANK urn:lsid:zoobank.org:act:2C214B38-5A6C-4A12-9FEF-0AD83DE968C3 Darrel's Chorus Frog

(Figures 1-3, 24, 25, 27, S1, S2; Tables S1-S5; File S1)

**Etymology.** The species is named after Dr. Darrel R. Frost, an American herpetologist, in recognition of his contribution "Amphibian Species of the World, an online

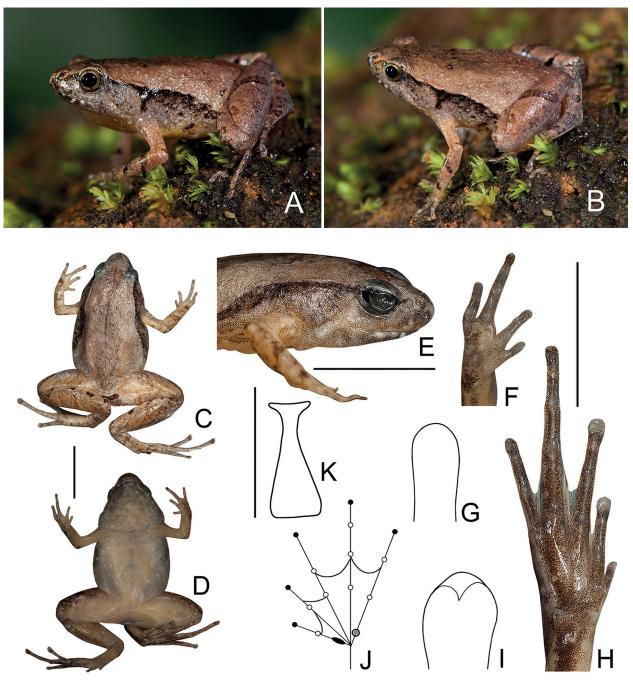
database" to amphibian research. The species name *darreli* is used as a noun in the genitive case.

**Holotype.** ZSI/WGRC/V/A/961, an adult male, from Karamana, (8.4506°N, 76.9752°E, 21 m asl), Thiruvananthapuram district, Kerala state, India, collected by SD Biju, Sonali Garg, and Robin Suyesh on 1 July 2015.

**Paratypes.** ZSI/WGRC/V/A/962–965, four adult males, collected along with the holotype.

**Other referred specimens.** SDBDU 2015.2976, an adult male, collected along with the holotype, and SDBDU 2009.101, an adult male, from Chathankodu, Thiruva-nanthapuram district, Kerala state, India, collected by RS and SDB on 16 July 2009.

Description of holotype (measurements in mm) (Fig. 27). A small-sized adult male (SVL 15.1), rather slender; head wider than long (HW 4.3, HL 4.1); snout subovoid in dorsal view, rounded in lateral view, its length (SL 1.9) longer than horizontal diameter of eye (EL 1.3); loreal region vertical, indistinct canthus rostralis; interorbital space flat, wider (IUE 1.6) than upper eyelid width (UEW 0.8) and internarial distance (IN 1.1); nostrils oval, placed more towards dorsal side of snout, closer to snout (NS 0.7) than eye (EN 0.9); tympanum indistinct; supratympanic fold extending from posterior corner of eye to the shoulder weakly-developed; vomerine teeth absent; tongue small, oval, without papillae. Arms short, forearm length (FAL 2.5) shorter than hand length (HAL 3.7); relative length of fingers I< IV< II< III (FL<sub>I</sub> 0.7, FL<sub>II</sub> 1.4, FL<sub>III</sub> 2.5, FL<sub>IV</sub> 1.3); tips of all fingers



**Fig. 27.** Holotype of *Microhyla darreli* **sp. nov.** (ZSI/WGRC/V/A/961), a newly described member of the *Microhyla zeylanica* species group. **A.** Dorsolateral view. **B.** Dorsolateral view (A–B, in life). **C.** Dorsal view. **D.** Ventral view. **E.** Lateral view of head. **F.** Ventral view of hand. **G.** Third finger tip. **H.** Ventral view of foot. **I.** Fourth toe tip. **J.** Schematic illustration of webbing on foot. **K.** Terminal phalanx of fourth toe (C–K, in preservation). (Photographs: S. D. Biju).

without grooves, finger tips slightly wider compared to finger width (FD<sub>1</sub>0.4; FW<sub>1</sub>0.3, FD<sub>II</sub> 0.4; FW<sub>II</sub> 0.3, FD<sub>II</sub> 0.4; FW<sub>II</sub> 0.3, FD<sub>IV</sub> 0.3, FD<sub>IV</sub> 0.3); dermal fringes weakly-developed, webbing absent between fingers; sub-articular tubercles rather prominent; outer and inner palmar tubercles weakly developed; supernumerary tubercles absent; nuptial pad absent. Hind limbs short, thigh (TL 7.3) shorter than shank (SHL 8.3) and foot (FOL 8.0); distance from base of tarsus to tip of toe IV (TFOL 11.8); relative length of toes I< II< III< V< IV; toe tips rounded, slightly enlarged into discs (TD<sub>1</sub>0.4; TW<sub>1</sub>0.4,

 $TD_{II}$  0.5;  $TW_{II}$  0.4,  $TD_{III}$  0.6;  $TW_{III}$  0.4,  $TD_{IV}$  0.6,  $TW_{IV}$  0.3,  $TD_{V}$  0.5,  $TW_{V}$  0.3); toe discs with prominent dorsoterminal grooves, cover bifurcate distally; toes with dermal fringes; terminal phalanges of toes T-shaped; foot webbing:  $I2-2^{+}II2^{-}-3III2-3IV3-2^{1}/_{4}V$ ; subarticular tubercles prominent, all present, circular; inner metatarsal tubercle prominent (IMT 0.6), oval-shaped; outer metatarsal tubercle, small (OMT 0.3), rounded; supernumerary tubercles absent.

Skin of snout shagreened, upper eyelids shagreened to sparsely granular; anterior and posterior parts of dor-

sum shagreened to sparsely granular; upper and lower parts of flank shagreened; presence of a narrow middorsal skin fold or line extending from tip of the snout to the vent; presence of a prominent dark blackish-brown lateral band, marking, or skin fold starting from tip of the nostril and approaching the groin on either side of the body; dorsal surfaces of forelimbs, thighs, and shanks shagreened; ventral surfaces of throat, chest, belly, and limbs smooth (Fig. 27).

Color of holotype. In life. Dorsum, upper eyelids, and lateral surfaces of snout greyish-brown, scattered light brown markings on anterior parts of dorsum and snout (Fig. 27); lateral surfaces of head light greyish-brown with minute light brown spots; upper and lower lip with prominent brown cross-bands; lateral side of abdomen greyish-brown with a dark blackish-brown band, marking, or skin fold starting from tip of the nostril and approaching the groin; a dark blackish-brown crescentshaped marking above the cloacal opening; forelimbs and hind limbs (including toes) light greyish-brown with brown transverse bands; webbing light brown; anterior parts of thigh light yellowish-brown with faint grey spots. Ventral surface of throat light flesh color with minute dark brown speckles; belly white; forearms and forelegs light flesh red in color with dark brown mottling on the margins. In preservation. Dorsum light greyishbrown; forelimbs and hind limbs light grey with dark greyish-brown transverse bands; fingers yellowish-white with minute dark brown speckles on the third and fourth fingers. Ventral surface of throat light grey with dark grey speckles; belly light grey; margins of the limbs light grey with greyish-brown mottling (Fig. 27).

**Morphological variations.** Morphometric data from six adult males is given in Table S5. ZSI/WGRC/V/A/963 and ZSI/WGRC/V/A/965: dorsum with more prominent dark grey markings; ZSI/WGRC/V/A/964: dorsum with slightly more scattered granular projections than the holotype.

Secondary sexual character. Males with single median vocal sacs.

**Morphological comparison.** *Microhyla darreli* **sp. nov.** could be confused with *M. karunaratnei*, *M. laterite*, *M. sholigari*, and *M. zeylanica* within the *Microhyla zeylanica* group. However, *Microhyla darreli* **sp. nov.** clearly differs from *M. karunaratnei* by its ventral surfaces being uniformly light grey (vs. creamy white with promiment black spots and mottling) and throat grey (vs. with dark blackish-brown mottling). It further differs from *M. karunaratnei* by its loreal region vertical (vs. oblique) and snout rounded in lateral view (vs. rounded to vertical). It differs from *M. laterite* by lesser webbing on the first and second toes,  $I2-2^+II2^-3III2-3IV3 2^{1/4}V$  (vs. more, I1-2II1-3III2-3IV3-2V), and outer metatarsal tubercles relatively weak (vs. relatively more developed). It differs from *M. sholigari* by its relatively smaller adult male size, SVL 15-16 mm, N=6 (vs. larger: SVL 16-18 mm, N=5), snout subovoid in dorsal and ventral views, rounded in lateral view (vs. subelliptical to nearly pointed in dorsal view, rounded to nearly acute in lateral view), and fourth toe webbing extending up to the second subarticular tubercle on either side,  $I2-2^{+}II$  $2^{-}-3III2-3IV3-2^{1}/_{4}V$  (vs. below,  $I2^{-}-2II1^{1}/_{2}-3^{-}III2 3^{+}IV3^{+}-2V$ ). It differs from *M. zeylanica* by its dorsum vellowish-brown (vs. light or dark reddish-brown), presence of a dark blackish-brown lateral band or marking with weakly developed skin fold starting from tip of the nostril and approaching the groin on either side of the body (vs. absence of dark blackish-brown lateral band or markings but presence of well-developed glandular skin fold starting from tip of the nostril and approaching the groin on either side of the body), shank nearly equal to foot length, male SHL 8.1-8.4 mm, FOL 7.9-8.2 mm, N=6 (vs. shorter, male SHL 8.3-8.8 mm, FOL 9.2-9.9 mm, N=4), and toe discs with prominent dorso-terminal grooves, cover bifurcate distally (vs. with circum-marginal grooves).

Further, the new species differs from other known South Asian members of the genus by its nostrils placed more towards the dorsal side of the snout (vs. laterally placed). More specifically, it differs from M. chakrapanii, M. mukhlesuri, M. mymensinghensis, M. mihintalei, M. nilphamariensis, M. ornata, and M. rubra by toe discs with dorso-terminal grooves (vs. rounded without grooves); from M. cf. heymonsi by absence of '()' shaped marking on the dorsum (vs. present), ventral surfaces of foot grey (vs. ventral surface of foot up to knee prominently dark brown), and small foot webbing, up to second subarticular tubercle on either side of toe IV, formula  $I2-2^{+}II2^{-}-3III2-3IV3-2^{1}/_{4}V$  (vs. rudimentary,  $I2-2^{3}/_{4}$ +II2-3III3-4IV4-3V); from *M. berdmorei* by its smaller adult male size, SVL 15–16 mm, N=6 (vs. larger, male SVL 33-36 mm, N=6), terminal phalanges of toes T-shaped (vs. Y-shaped), and small foot webbing, up to second subarticular tubercle on either side of toe IV, formula  $I2-2^{+}II2^{-}-3III2-3IV3-2^{1}/_{4}V$  (vs. large, extending up to the discs,  $I1 - 1II1 - 1^{+}III1 - 1^{1}/_{2}IV1^{1}/_{2} - 1$ V); from *M. kodial* by its dorsal skin shagreened without prominent granular projections (vs. shagreened to granular), presence of a narrow mid-dorsal skin fold or line extending from tip of the snout to the vent (vs. absent), presence of a dark blackish-brown lateral band, marking, or skin fold starting from tip of the nostril and approaching the groin on either side of the body (vs. absent), and small foot webbing, up to second subarticular tubercle on either side of toe IV, formula I2-2+II2-3III2-3IV3-2  $\frac{1}{4}$ V (vs. rudimentary,  $I2-2^{1}/_{2}+II2-3III3-4IV4-3V$ ).

**Genetic comparison.** Phylogenetically, *Microhyla darreli* **sp. nov.** is closely related to members of the *Microhyla zeylanica* group (Figs. 1, 24) and differs by the following uncorrected genetic distances for the 16S gene: *M. karunaratnei* (2.5%), *M. laterite* (3.8-4.2%), *M. sholigari* (3.1-3.3%), and *M. zeylanica* (5.0%) (Table S2). **Vocalization.** The calls of *Microhyla darreli* **sp. nov.** (SD-BDU 2009.101) were recorded at Chathankod, by RS and Mark Bee on 16 July 2009, between 20:00-20:30 h, at air temperature:  $25.6^{\circ}$ C dry bulb,  $25.4^{\circ}$ C wet bulb. The male produced a single type of call with pulsatile temporal structure. The calls were not delivered in groups and had uniform intervals. Calls were relatively long with a mean duration of 653.8 ms (590.3–736.2 ms) with 68 pulses (63–78 pulses) delivered at a rate of 105.6 pulses/s (103.9–106.7 pulses/s), rise time of 516.4 ms (468.6–651.3 ms), and fall time of 97.2 ms (63.8–131.8 ms). The call spectrum was characterized by a single broad peak with mean dominant frequency of 3.6 kHz (Fig. 25; Table S4).

Acoustic comparison. Overall, the calls of *Microhyla darreli* sp. nov. were similar to species in the *Microhyla zeylanica* group. However, *M. darreli* calls were the shortest among all, 590.3–736.2 ms (vs. 766.3–1003.1 ms in *M. karunaratnei*, 727.1–886.4 ms in *M. laterite*, 901.1–1012.4 ms in *M. sholigari*, and 1705.2–1804.3 ms in *M. zeylanica*). This species also delivered calls at a faster rate of 103.9–106.7 pulses/s (vs. slower, 72.2–81.5 pulses/s in *M. karunaratnei*, 76.9–77.8 pulses/s in *M. sholigari*, and 47.1–49.6 pulses/s in *M. zeylanica*), while the pulse rate was slower compared to *M. laterite* (126.3–129.5 pulses/s) (Fig. 25; Table S4).

Distribution and natural history. Microhyla darreli sp. nov. is currently known only from regions south of Palghat gap in the Western Ghats state of Kerala (Fig. 24). Apart from the type locality Karamana, its presence was also confirmed at Chathankod, located approximately 50 km northeast of the type locality in the same district (Thiruvananthapuram district). During the monsoon season in the months of June-July, a large number of individuals were observed inside a wayside plantation area at a rural settlement close to the Karamana River. This species occurs sympatrically with M. ornata, and the two were also observed calling alternatively at the same site (average inter-male distance of 1-2 feet). Calling males of M. darreli were usually observed hiding under leaf litter or ground vegetation, while males of M. ornata were relatively more exposed. The Chathankod population was found adjacent to a temporary pool of water inside a plantation and the specific site was located at a tribal settlement on forest edges. This species was found to be locally abundant during its short breeding season (June–July).

# *Microhyla karunaratnei* Fernando & Siriwardhane, 1996

Karunaratne's Narrow-mouth Frog (DE SILVA, 2009)

(Figures 1-3, 24, 25, 28, S1, S2; Tables S1-S5; File S1)

Original name and description. *Microhyla karunaratnei* FERNANDO P. & SIRIWARDHANE M. 1996. *Microhyla*  *karunaratnei* (Anura: Microhylidae), a new species of frog endemic to Sri Lanka, *Journal of South Asian Natural History* 2: 135–142. **Type.** Holotype AMS R 148277, by original designation. **Type locality.** "Morningside Estate, Sinharaja World Heritage Site", Sri Lanka. **Current status of specific name.** Valid name, as *Microhyla karunaratnei* Fernando & Siriwardhane, 1996.

**Description of holotype.** A detailed description is available (Fernando & Siriwardhane, 1996).

Morphological comparison. Microhyla karunaratnei differs from all other South Asian Microhyla groups, except members of the Microhyla zevlanica group, by its nostrils placed more towards the dorsal side of the snout (vs. placed laterally), ventral surfaces creamy white with prominent black spots and throat with dark blackishbrown mottling (vs. ventral surfaces light grey or offwhite and throat grey). Morphologically, M. karunaratnei could be confused with M. darreli sp. nov., M. laterite, M. sholigari, and M. zeylanica within the Microhyla zeylanica group. However, it differs from all these species by relatively more webbing on foot, third toe webbing extending up to the first subarticular tubercle on the inside, I1-2II1-2III2-3IV3-2V (vs. below or up to the second subarticular tubercle in all other species), ventral surfaces creamy white with prominent black spots and throat with dark blackish-brown mottling (vs. without prominent spots or mottling) (Fig. 28). See M. darreli for comparison with that species.

**Genetic comparison.** Phylogenetically, *Microhyla karunaratnei* is closely related to members of the *Microhyla zeylanica* group (Figs. 1, 24) and differs from them by the following uncorrected genetic distances for the 16S gene: *M. darreli* **sp. nov.** (2.5%), *M. laterite* (3.7–4.0%), *M. sholigari* (4.4–4.6%), and *M. zeylanica* (5.2%) (Table S2).

**Vocalization.** The calls of *Microhyla karunaratnei* (DZ 1530) were recorded at Morningside forest reserve, Suriyakanda, Rathnapura district, by MM and team on 9 December 2014, between 20:00-23:00 h, at air temperature:  $19.1^{\circ}$ C dry bulb,  $17.5^{\circ}$ C wet bulb. The males produced single type of call with pulsatile temporal structure. The calls were not delivered in groups and had uniform intervals. A typical advertisement call had a mean duration of 869.4 ms (766.3–1003.1 ms) with 60 pulses (56–86 pulses) delivered at a rate of 76.1 pulses/s (72.2–81.5 pulses/s), rise time of 647.4 ms (519.3–872.9 ms), and a short fall time of 141.4 ms (98.1–175.7 ms). The call spectrum was characterized by two broad peaks with the overall mean dominant frequency of 3.2 kHz (Fig. 25; Table S4).

Acoustic comparison. Overall, the calls of *Microhyla karunaratnei* were similar to species in the *Microhyla zeylanica* group. However, *M. karunaratnei* calls had the least number of pulses, 56–86 pulses (vs. 63–78

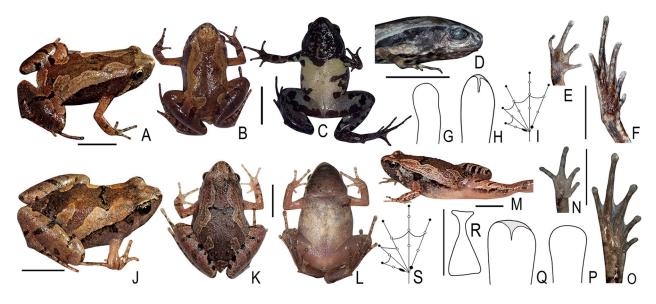


Fig. 28. Morphological characters of two species in the *Microhyla zeylanica* species group. A–I. *Microhyla karunaratnei*. A. Dorsolateral view. B. Dorsal view. C. Ventral view (A–C, in life, voucher DZ 1530). D. Lateral view of head. E. Ventral view of hand. F. Ventral view of foot. G. Third finger tip. H. Fourth toe tip. I. Schematic illustration of webbing on foot (D–I, in preservation, voucher DZ 1530). J–S. *M. laterite*. J. Dorsolateral view (in life, voucher SDBDU 2015.3063). K. Dorsal view. L. Ventral view. M. Lateral view of head (K–M, in life, voucher SDBDU 2017.3602). N. Ventral view of hand. O. Ventral view of foot. P. Third finger tip. Q. Fourth toe tip. R. Terminal phalanx of fourth toe. S. Schematic illustration of webbing on foot (N–S, in preservation, voucher SDBDU 2017.3699). Scale bars: 5 mm. (Photographs: S. D. Biju; A–C, N. Wijayathilaka).

in *M. darreli* **sp. nov.**, 94–113 in *M. laterite*, 70–79 in *M. sholigari*, and 81–90 in *M. zeylanica*). As shown previously (WIJAYATHILAKA & MEEGASKUMBURA, 2016), within the group, *M. karunaratnei* calls showed close resemblance with calls of *M. sholigari*, with respect to all the studied call properties (Fig. 25; Table S4). Compared to the other Sri Lankan counterpart, *M. zeylanica*, the calls of *M. karunaratnei* were much shorter in duration 766.3–1003.1 ms (vs. 1705.2–1804.3 ms) and had faster pulse rate of 72.2–81.5 pulses/s (vs. 47.1–49.6 pulses/s).

**Distribution and natural history.** This species is currently known to have a narrow distribution and is restricted to wet evergreen forests at Morningside forest reserve, at elevations of around 1,100 m asl. At night, calling individuals were found on wet leaf litter on edges of shrubcovered pools. Many of these isolated pools were 1-2 m in depth containing clear water with a muddy substrate.

#### *Microhyla laterite* Seshadri, Singal, Priti, Ravikanth, Vidisha, Saurabh, Pratik & Gururaja, 2016

Laterite Narrow-mouthed Frog (SESHADRI et. al., 2016A)

(Figures 1–3, 24, 25, 28, S1, S2; Tables S1–S5; File S1)

**Original name and description.** *Microhyla laterite* Seshadri K. S., Singal R., Priti G. H., Ravikanth M., Vidisha K., Saurabh S., Pratik M. & Gururaja. K.V. 2016. *Microhyla laterite* sp. nov., a new species of *Microhyla* Tschu-

SENCKENBERG

di, 1838 (Amphibia: Anura: Microhylidae) from a laterite rock formation in South West India, *PLoS One* 11(3): e0149727. **Type.** Holotype BNHS 5964, by original designation. **Type locality.** "from laterite rocks in Kodanga, Herga village, Manipal, Udupi District", India. **Current status of specific name.** Valid name, as *Microhyla laterite* Seshadri, Singal, Priti, Ravikanth, Vidisha, Saurabh, Pratik & Gururaja, 2016.

**Description of holotype.** A detailed description is available (SESHADRI *et al.*, 2016A).

Morphological comparison. Microhyla laterite could be confused with Microhyla darreli sp. nov., M. karunaratnei, M. sholigari, and M. zeylanica within the Microhyla zeylanica group. However, it differs from M. sholigari and *M. zeylanica* by webbing on toe I extending up to the disc (vs. lesser, not beyond the first subarticular tubercle). More specifically, it differs from *M. zeylanica* by its toe discs with prominent dorso-terminal grooves, cover bifurcate distally (vs. toe discs with circum-marginal grooves), and presence of a dark blackish-brown lateral band with weakly-developed skin fold starting from tip of the nostril and approaching the groin on either side of the body (vs. absence of blackish-brown lateral band or markings with well-developed glandular skin fold starting from tip of the nostril and approaching the groin on either side of the body) (Fig. 28). See Microhyla darreli sp. nov. and *M. karunaratnei*, for comparison with those species.

Further, *Microhyla laterite* differs from members of the other South Asian groups by combination of follow-

ing characters: relatively smaller adult male size, SVL 14-17 mm, N=5 (vs. larger, except *M. kodial*), nostrils placed more towards the dorsal side of the snout (vs. placed laterally), and toe discs with prominent dorso-terminal grooves and cover bifurcate distally (vs. toe discs without dorso-terminal grooves, except *M. kodial*). For differences with *M. kodial*, see comparison of that species.

**Genetic comparison.** Phylogenetically, *Microhyla laterite* is closely related to members of the *Microhyla zeylanica* group (Figs. 1, 24) and differs from them by the following uncorrected genetic distances for the 16S gene: *M. darreli* **sp. nov.** (3.8-4.2%), *M. karunaratnei* (3.7-4.0%), *M. sholigari* (4.2-4.6%), and *M. zeylanica* (3.8-4.6%) (Table S2). Within the *M. laterite* clade (Fig. 24), populations from northern Kerala (Anakallu village and Madayipara) showed intraspecific divergence of up to 1.3% from the typical populations of Manipal in Karnataka (Table S2).

**Vocalization.** The calls of *Microhyla laterite* (SDBDU 2015.3062) were recorded at Manipal, by SDB and SG on 13 July 2015, between 20:00-20:30 h, at air temperature: 27.0°C dry bulb, 26.5°C wet bulb. The male produced a single type of call with pulsatile temporal structure. The calls were not delivered in groups and had uniform intervals. Calls were relatively long with a mean duration of 809.6 ms (727.1–886.4 ms) with 104 pulses (94–113 pulses) delivered at a rate of 128 pulses/s (126.3–129.5 pulses/s), rise time of 673.4 ms (542.1–823.8 ms), and fall time of 80.4 ms (62.4–111.8 ms). The call spectrum was characterized by a single broad peak with mean dominant frequency of 3.6 kHz (Fig. 25; Table S4).

Acoustic comparison. Overall, the calls of *Microhyla laterite* were similar to species in the *Microhyla zey-lanica* group. However, *M. laterite* calls had a relatively shorter fall time among all the members, 62.4-111.8 ms (vs. 63.8-131.8 ms in *M. darreli* sp. nov., 98.1-175.7 ms in *M. karunaratnei*, 115.8-177.1 ms in *M. sholigari*, and 602.4-976.8 ms in *M. zeylanica*), which gave it the highest call rise and call fall time ratio of 9.1:1.0 (Fig. 25; Table S4). The calls of *M. laterite* were also distinct from other studied South Asian species because of their fastest pulse rate of 126.3-129.5 pulses/s. For comparison with *Microhyla darreli* sp. nov. and *M. karunaratnei*, see the acoustic comparison section of those species.

Our call recordings of *M. laterite* from the type locality Manipal were similar to those reported by SESHADRI *et al.* (2016A) in the various analysed call properties.

**Distribution and natural history.** *Microhyla later-ite* is currently known only from regions north of Palghat gap in the Western Ghats of India. This species was originally described from Manipal, Udupi District (13.2868°-13.3757° N and 74.7795°-74.8731° E, 50 m asl), Karnataka state. In this study, we also report the presence of *M. laterite* in northern Kerala (Anakallu village and Madayipara) (Fig. 24; Table S1). The populations at Manipal and Madayipara were observed adjacent to water bodies in laterite habitats, whereas at the Anakallu village actively calling individuals were observed on edges of a water-logged cultivated area. At all the three locations, *M. laterite* was found sympatrically with *M. nilphamariensis*, and the two were also observed calling alternatively at the same site (average inter-male distance of 2 m at Manipal, 1 m at Anakallu, and 4 m at Madayipara).

#### Microhyla sholigari Dutta & Ray, 2000

Sholiga Narrow-mouthed Frog (SESHADRI *et. al.*, 2016B) (Figures 1–3, 24, 25, 29, S1, S2; Tables S1–S5; File S1)

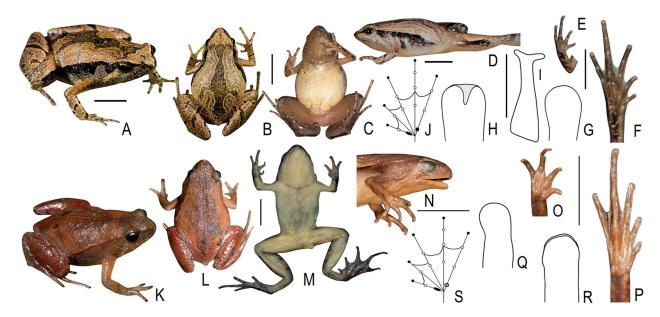
**Original name and description.** *Microhyla sholigari* Dutta S. K. & Ray P. 2000. *Microhyla sholigari*, a new species of microhylid frog (Anura: Microhylidae) from Karnataka, India, *Hamadryad* 25: 38–44. **Type.** Holotype ZSIC A9061, by original designation. **Type locality.** "Bhargavi stream bed near Doddasampige (12°27'N; 76°11' E, Biligirirangan Hills, Chamrajanagar District, Yelandur Taluk, Karnataka State, south-western India", India. **Current status of specific name.** Valid name, as *Microhyla sholigari* Dutta & Ray, 2000.

**Description.** A detailed description of the holotype (DU-TTA & RAY, 2000) and a redescription of the species based on topotypes (SESHADRI *et al.*, 2016B) are available.

**Morphological comparison.** *Microhyla sholigari* could be confused with *Microhyla darreli* **sp. nov.**, *M. karunaratnei*, *M. laterite*, and *M. zeylanica* within the *Microhyla zeylanica* group. However, it differs from *M. zeylanica* by toe discs with prominent dorso-terminal grooves, cover bifurcate distally (vs. toe discs with circum-marginal grooves), and presence of a dark blackish-brown lateral band with weakly-developed skin fold starting from tip of the nostril and approaching the groin (vs. absence of blackish-brown lateral band or markings with well-developed glandular skin fold starting from tip of the nostril and approaching the groin) (Fig. 29). See *Microhyla darreli* **sp. nov.**, *M. karunaratnei*, and *M. laterite* for comparison with those species.

Further, *Microhyla sholigari* differs from members of the other South Asian groups by combination of following characters: relatively smaller adult male size, SVL 16–18 mm, N=5 (vs. larger, except *M. kodial*), nostrils placed more towards the dorsal side of the snout (vs. placed laterally), and toe discs with prominent dorso-terminal grooves, cover bifurcate distally (vs. toe discs without dorso-terminal grooves, except *M. kodial*). For differences with *M. kodial*, see comparison of that species.

**Genetic comparison.** Phylogenetically, *Microhyla sholigari* is closely related to members of the *Microhyla zeylanica* group (Figs. 1, 24) and differs from them by



**Fig. 29.** Morphological characters of two species in the *Microhyla zeylanica* species group. **A–J.** *Microhyla sholigari*. **A.** Dorsolateral view (in life, SDBDU 2014.2531). **B.** Dorsal view (in life, SDBDU 2014.2532). **C.** Ventral view. **D.** Lateral view of head (C–D, in life, SDBDU 2016.3440). **E.** Ventral view of hand. **F.** Ventral view of foot. **G.** Third finger tip. **H.** Fourth toe tip. **I.** Terminal phalanx of fourth toe. **J.** Schematic illustration of webbing on foot (E–J, in preservation, SDBDU 2014.2531). **K–S.** *M. zeylanica.* **K.** Dorsolateral view. **L.** Dorsal view (K–L, in life, voucher DZ 1421). **M.** Ventral view (in preservation, voucher DZ 1421). **N.** Lateral view. **O.** Ventral view of hand. **P.** Ventral view of foot. **Q.** Third finger tip. **R.** Fourth toe tip. **S.** Schematic illustration of webbing on foot (N–S, in preservation, BMNH 1948.1.1.3, Holotype). Scale bars: 5 mm. (Photographs: S. D. Biju; A–C, S. Garg; K–L, M. Meegaskumbura).

the following uncorrected genetic distances for the 16S gene: *M. darreli* **sp. nov.** (3.1-3.3%), *M. karunaratnei* (4.4-4.6%), *M. laterite* (4.2-4.6%) and *M. zeylanica* (5.4-5.8%). Within *M. sholigari*, populations showed shallow intraspecific distances of up to 0.4% (Table S2).

**Vocalization.** The calls of *Microhyla sholigari* (SDBDU 2014.2537) were recorded at Biligirirangan Hills, by SDB and SG on 23 July 2014, between 18:00-20:00 h, at air temperature:  $26.5^{\circ}$ C dry bulb,  $26.5^{\circ}$ C wet bulb. The male produced a single type of call with pulsatile temporal structure. The calls were not delivered in groups and had uniform intervals. Calls were relatively long with a mean duration of 933.4 ms (901.1–1012.4 ms) with 72 pulses (70–79 pulses) delivered at a rate of 77.3 pulses/s (76.9–77.8 pulses/s), rise time of 728.8 ms (662.9–843.7 ms), and fall time of 149.1 ms (115.8–177.1 ms). The call spectrum was characterized by a single broad peak with mean dominant frequency of 3.4 kHz (Fig. 25; Table S4).

Acoustic comparison. Overall, the calls of *Microhyla sholigari* were similar to species in the *Microhyla zeylanica* group. However, compared to other Indian members, *M. sholigari* calls were the longest in duration, 901.1–1012.4 ms (vs. 590.3–736.2 ms in *M. darreli* sp. nov. and 727.1–886.4 ms in *M. laterite*) (Fig. 25; Table S4). Compared to the Sri Lankan species, *M. zeylanica*, it also had a faster pulse rate of 76.9–77.8 pulses/s (vs. slower, 47.1–49.6 pulses/s). For comparison with *Microhyla darreli* sp. nov., *M. karunaratnei*, and *M. laterite*, see the acoustic comparison section of those species.

We also compared our call recordings of *M. sholigari* with those reported by SESHADRI *et al.* (2016B). While our calls showed a duration ranging between 901.1–1012.4 ms (Table S4), SESHADRI *et al.* (2016B) reported a range of 530.0-810.0 ms.

Distribution and natural history. Microhyla sholigari was originally described from Biligirirangan Hills, based on subadult specimens that include the holotype (ZSI A9061, SVL 10.8 mm) and four paratypes. Subsequently, BIJU et al. (2004) reported this species from Wayand Wildlife Sanctuary (requires confirmation), VAN BOCX-LAER et al. (2006) and HASAN et al. (2014B) reported DNA sequences (as M. 'ornata'), and SESHADRI et al. (2016B) discussed its extended distribution range based on additional records within Karnataka state, with an elevation range of 650-1200 m asl. Here, we further confirm the presence of this species in Tamil Nadu (Masinagudi, which is also the southernmost record) and three additional localities in Karnataka (Bhagamandala, Gundalpetta, and Shimoga — the latter being the northernmost record so far) (Fig. 24; Table S1). This species is usually found close to water bodies, either under wayside vegetation or waterlogged areas in secondary forest patches. At Biligirirangan Hills, this species was observed sympatrically with M. ornata and M. rubra, with all three species breeding within close proximity.

**Notes.** This species could be confused or considered conspecific with a previously available name, *Engystoma malabaricum* Jerdon, 1853 currently under the synonymy of *Microhyla ornata*. For detailed discussion, see the "notes" under *M. ornata*.

#### Microhyla zeylanica Parker & Osman-Hill, 1949

Sri Lanka Narrow-mouth Frog (DE SILVA, 2009)

(Figures 1-3, 24, 25, 29, S1, S2; Tables S1-S5; File S1)

**Original name and description.** *Microhyla zeylanica* Parker H. W. & Osman-Hill W. C. 1949. Frogs of the genus *Microhyla* from Ceylon, *Annals and Magazine of Natural History* 12 (1): 759–764. **Type.** Holotype NHM 1948.1.1.3, by original designation. **Type locality.** "In the 'Bopats' (Bopatalawa) and Horton Plains .... Bopatalawa, Central Province, alt. 6000 ft. Caught near pool in compound of the Irrigation Dept. bungalow ...", Sri Lanka. **Current status of specific name.** Valid name, as *Microhyla zeylanica* Parker & Osman-Hill, 1949.

**Description of holotype.** A detailed description of holotype is available (PARKER & OSMAN-HILL, 1949).

**Morphological comparison.** *Microhyla zeylanica* could be confused with *M. darreli* **sp. nov.**, *M. karunaratnei*, *M. laterite*, and *M. sholigari* within the *Microhyla zeylanica* group. However, it differs from all these members by toe discs with circum-marginal grooves (vs. with dorso-terminal grooves, cover bifurcate distally), and absence of blackish-brown lateral band or markings with well-developed glandular skin fold starting from tip of the nostril and approaching the groin (vs. presence of a dark blackish-brown lateral band or marking with weak-ly-developed skin fold starting from tip of the nostril and approaching the groin (vs. presence of a dark blackish-brown lateral band or marking with weak-ly-developed skin fold starting from tip of the nostril and approaching the groin) (Fig. 29). See *M. darreli* **sp. nov.**, *M. karunaratnei, M. laterite*, and *M. sholigari* for comparison with those species.

Further, *Microhyla zeylanica* differs from members of the other South Asian groups by combination of following characters: relatively smaller adult male size, SVL 17-20 mm, N=4 (vs. larger, except *M. kodial*), nostrils placed more towards the dorsal side of the snout (vs. placed laterally), toe discs with circum-marginal grooves (vs. without circum-marginal grooves), well-developed glandular skin fold starting from tip of the nostril and approaching the groin and absence of blackish-brown lateral band or markings (vs. presence of lateral band or markings with weakly-developed skin fold starting from tip of the nostril and approaching the groin, except in *M. kodial*). For differences with *M. kodial*, see comparison of those species.

**Genetic comparison.** Phylogenetically, *Microhyla zeylanica* is closely related to members of the *Microhyla zeylanica* group (Figs. 1, 24) and differs from them by the following uncorrected genetic distances for the 16S gene: *M. darreli* **sp. nov.** (5.0%), *M. karunaratnei* (5.2%), *M. laterite* (3.8–4.6%), and *M. sholigari* (5.4–5.8%) (Table S2). **Vocalization.** The calls of *Microhyla zeylanica* (DZ 1420) were recorded at Horton Plains National Park, by MM and team on 25 August 2014, between 21:00-22:00 h, at air temperature:  $18.2^{\circ}$ C dry bulb,  $17^{\circ}$ C wet bulb. The male produced a single type of call with pulsatile temporal structure. The calls were not delivered in groups and had uniform intervals. Calls were relatively long with mean duration of 1759.5 ms (1705.2–1804.3 ms) with 86 pulses (81–90 pulses) delivered at a rate of 48.4 pulses/s (47.1–49.6 pulses/s), rise time of 870.5 ms (609.4–1074.3 ms), and relatively shorter fall time of 773.3 ms (602.4–976.8 ms). The call spectrum was characterized by two broad peaks with the overall mean dominant frequency of 2.7 kHz (Fig. 25; Table S4).

Acoustic comparison. *Microhyla zeylanica* differed considerably from all other species in the *Microhyla zeylanica* group as well as studied members of other South Asian groups mainly by its longest call duration, 1705.2– 1804.3 ms (Fig. 25; Table S4). For detailed comparison with *M. darreli* **sp. nov.**, *M. karunaratnei*, *M. laterite*, and *M. sholigari*, see the acoustic comparison section of those species.

**Distribution and natural history.** *Microhyla zeylanica* is currently restricted to wet evergreen forests of Horton Plains National Park, at elevations of around 2,100 m asl (Fig. 24). At night, vocalizing individuals were found at the edges of shallow pools (< 0.3 m in depth) in an open grassland. The grass was emergent in most areas of the pools, which had a muddy substrate but contained clear water. Calling frogs were extremely sensitive to vibrations and stopped calling when approached; sometimes taking up to 20 minutes to resume calling.

#### Discussion

Our study recognizes 16 Microhyla species in South Asia and of these 13 are restricted to regions within South Asia (M. chakrapanii, M. darreli sp. nov., M. karunaratnei, M. kodial, M. laterite, M. mihintalei, M. mymensinghensis, M. nilphamariensis, M. ornata, M. rubra, M. sholigari, M. taraiensis, and M. zeylanica) and three are also found in Southeast Asia (M. berdmorei, M. cf. heymonsi, and M. mukhlesuri). Patterns of species distribution were largely in congruence with geographical ranges of the six recognized South Asian species groups: the Microhyla rubra group and Microhyla zeylanica group are only found in Peninsular India and Sri Lanka; the Microhyla ornata group is the most wide-ranging group of South Asia; the Microhyla fissipes group has wider distributions in South, Southeast Asia, and East Asia; and the remaining two groups (Microhyla achatina group and Microhyla berdmorei group) are largely Southeast Asian radiations with only one South Asian representative each. Furthermore, we tentatively include M. kodial in the Mi*crohyla achatina* group, though the species exhibits several unique characters and its phylogenetic position remains poorly resolved. The observed patterns of genetic and morphometric differentiation within the *Microhyla fissipes* group also point the need for further taxonomic investigations since members of this group shared considerable similarities.

Certain unexpected relationships between Peninsular Indian-Sri Lankan and Northeast Indian-Southeast Asian species are also observed. For example, M. kodial (Peninsular India) and M. cf. heymonsi (Andaman Islands) are most close to members of the Microhyla achatina group, which is largely restricted to Southeast and East Asia, and another Andaman species M. chakrapanii is close to the Microhyla fissipes group (South + Southeast Asia). Among the various groups, [Microhyla fissipes + (Microhyla ornata + Microhyla rubra)] groups were closely related to (Microhyla achatina + Microhyla berdmorei) groups, while members of the Microhyla zeylanica group (Peninsular India) showed closer affinities with geographically distant species (M. butleri and M. superciliaris) in South and Southeast Asia. Robust phylogenies with more extensive sampling of all known members of the genus *Microhyla* and dating estimates could provide better insights on diversification and distribution in this large radiation of Asian frogs.

Our study resolves long-standing taxonomic confusions concerning the identity and distribution range of several South Asian Microhyla species. The poorly known M. chakrapanii was considered close to members of the Microhyla achatina group (e.g., DUTTA, 1997; CHANDA, 2002), however, this species has a sister relationship with M. mymensinghensis of the Microhyla fissipes group, both genetically and morphologically. Previous reports of M. butleri, M. heymonsi, and M. rubra from regions in Northeast India are confirmed to be misidentifications based on morphological and/or acoustic comparisons. At the same time, the presence of M. berdmorei in Northeast India and a potential new species closely allied to M. heymonsi in the Andaman Islands was genetically and morphologically confirmed. Our analyses also suggest that the current number of recognized Microhyla species may be underestimated. Several distinct populations such as the six sub-clades of M. 'heymonsi' and two additional lineages previously indicated as M. "sp. 1" and M. "sp. 3" (MATSUI et al., 2011) in the Microhyla achatina group, one misidentified population of M. cf. berdmorei previously shown as "M. rubra" (PELOSO et al., 2016), and several populations known only from wrongly identified DNA sequences (e.g., KT851981 as M. pertigena, KC180049 as M. achatina), are all likely to represent either new species requiring formal description or previously named taxa that are either poorly studied or known only from morphological descriptions and reported specimens (e.g., BAIN & NGUYEN, 2004; POYARKOV et al., 2014).

Although, molecular evidence suggests higher diversity, species delineation within the entire radiation of *Microhyla* frogs based on genetic differentiation alone are insufficient and challenging because of considerable overlaps in the levels of intra- and interspecific genetic divergence. Therefore, a combination of metric and meristic characters as well as call parameters, as shown for the South Asian members in the present study, can be useful for diagnoses across all known *Microhyla* species. Such approaches will also aid a comprehensive revision of the entire *Microhyla* radiation, which is essential for gathering a better understanding of diversity and relationships within the group.

The present study has addressed several taxonomic concerns relating to all South Asian *Microhyla* frogs, however, gaps still exist regarding their affinities with members from other regions. The taxonomic clarifications, detailed diagnostic characters, delineation of species, and their geographical ranges presented in this study based on integrated evidence, will aid similar comprehensive revisions of *Microhyla* groups and species found outside the region, so that a better systematic understanding of this morphologically cryptic group can be achieved sooner in the near future.

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# References

- AMPHIBIAWEB: information on amphibian biology and conservation (2018). California: University of California, Berkeley (Accessed on 1 March 2018). Available at: www.amphibiaweb.org.
- ANANJEVA, N. B., BORKIN, L. J., DAREVSKY I. S. & ORLOV, N. L. (1988). Dictionary of amphibians and reptiles in five languages. – Amphibians and Reptiles. Moscow, Russky Yazyk Publishers.
- ANDERS, C. C. (2002). Class Amphibia (Amphibians), in: Schleich H. H., Kästle W. (eds) Amphibians and Reptiles of Nepal: Biology, Systematics, Field Guide. Ruggell, A. R. G. Gantner Verlag K. G.
- ANDERSON, J. (1871). A list of the reptilian accession to the Indian Museum, Calcutta from 1865 to 1870, with a description of some new species. *Journal of the Asiatic Society of Bengal*, 40, 12–39.
- ARINI, K., NOER, M. I., WULANDARI, A., AMALIA, R., & AULIANDINA, T. (2016). Temporal and spectral variation in advertisement call of males *Microhyla achatina* (Tschudi, 1838) are sufficient for individual discrimination. *AIP Conference Proceedings*, **1744**, 020032(1–7).
- BAIN, R. H. & NGUYEN, T. Q. (2004). Three new species of narrowmouthed frogs (genus *Microhyla*) from Indochina, with comments on *Microhyla annamensis* and *Microhyla palmipes*. *Copeia*, 2004, 507–524.
- BEE, M. A., SUYESH, R. & BIJU, S. D. (2013). Vocal behavior of the Ponmudi Bush Frog (*Raorchestes graminirupes*): repertoire and individual variation. *Herpetologica*, 69, 22–35.
- BIJU, S. D. (2001). A synopsis to the frog fauna of the Western Ghats, India. *ISBC- Occasional Publication*, 1, 1–24.
- BIJU, S. D., DUTTA, S. K., BHUDDHE, G. D., VASUDEVAN, K. & SRINI-VASULU, C. (2004). *Microhyla sholigari*. The IUCN Red List of Threatened Species 2004, e.T57893A11688938.
- BIJU, S. D., GARG, S., GURURAJA, K. V., SHOUCHE, Y. & WALUJKAR, S. A. (2014A). DNA barcoding reveals unprecedented diversity in Dancing Frogs of India (Micrixalidae, *Micrixalus*): a taxonomic revision with description of 14 new species. *Ceylon Journal of Science (Biological Sciences)*, **43**, 37–123.
- BIJU, S. D., GARG, S., MAHONY, S., WIJAYATHILAKA, N., SENEVI-RATHNE, G. & MEEGASKUMBURA, M. (2014B). DNA barcoding, phylogeny and systematics of Golden-backed frogs (*Hylarana*, Ranidae) of the Western Ghats-Sri Lanka biodiversity hotspot, with the description of seven new species. *Contributions to Zoology*, 83, 269–335.
- BLYTH, E. (1856 "1855"). Report for October Meeting 1855. Journal of the Asiatic Society of Bengal, 24, 720.
- BOULENGER, G. A. (1882). Catalogue of the Batrachia Salientia s. Ecaudata in the Collection of the British Museum. London, Taylor and Francis.
- BOURRET, R. (1942). *Les Batraciens de l'Indochine*. Hanoi, Institut Océanographique de l'Indochine.
- CHANDA, S. K., DAS, I. & DUBOIS, A. (2000). Catalogue of amphibian types in the collection of the Zoological Survey of India. *Hamadryad*, 25, 100–128.
- CHANDA, S. K. (2002). Handbook Indian Amphibians. Calcutta, Zoological Survey of India.
- CHANDRAMOULI, S. R., HARIKRISHNAN, S. & VASUDEVAN, K. (2011). Little known endemic frogs of the Andaman islands. *Froglog*, 98, 16–17.
- CHANDRAMOULI, S. R., KHAN, T., YATHIRAJ, R., DESHPANDE, N., YA-DAV, S., TEJPAL, C., DE GROOT, S. & LAMMES, I. (2015). Diversity of amphibians in Wandoor, South Andaman, Andaman and Nicobar Islands, India. *Alytes*, **32**, 47–54.
- CHARIF, R. A., WAACK, A. M. & STRICKMAN, L. M. (2010). Raven Pro 1.4 User's Manual. Ithaca, New York, Cornell Lab of Ornithology.
- CHRISTY, M. T., SAVIDGE, J. A. & RODDA, G. H. (2007). Multiple pathways for invasion of anurans on a pacific island. *Diversity* and Distributions, 13, 598–607.

- DAS, I. & DUTTA, S. K. (1998). Checklist of the amphibians of India, with English common names. *Hamadryad*, 23, 63–68.
- DE SILVA, A. (2009). Amphibians of Sri Lanka: A Photographic Guide to Common Frogs, Toads and Caecilians. Kandy, Privately published.
- DEVI, Y.B. & SHAMUNGOU, K. (2006). Amphibian fauna of Manipur State, India. Journal of Experimental Zoology, 9, 317–324.
- DEY, M., & GUPTA, A. (2000). Records of *Kaloula pulchra* (Gray, 1831) (Anura: Microhylidae) from Cachar district, Assam, northeast India. *Hamadryad*, 25, 214–215.
- DINESH, K. P., RADHAKRISHNAN, C., GURURAJA, K. V. & BHATTA, G. K. (2009). An annotated checklist of amphibian of India with some insights into the patterns of species discoveries, distribution and endemism. *Records of the Zoological Survey of India*, **302**, 1–153.
- DUBOIS, A. (1987 "1986"). Miscellanea taxinomica batrachologica (I). *Alytes*, **5**, 7–95.
- DUMÉRIL, A. M. C. & BIBRON, G. (1841). Erpétologie genérale ou histoire naturelle complète des reptiles. Volume 8. Paris, Librarie Enclyclopedique de Roret.
- DUTTA, S. K. (1997). Amphibians of India and Sri Lanka, (Checklist and Bibliography). Bhubaneswar, Odyssey Publishing House.
- DUTTA, S. K. & MANAMENDRA-ARACHCHI, K. (1996). The Amphibian fauna of Sri Lanka. Colombo, Wildlife Heritage Trust of Sri Lanka.
- DUTTA, S. K. & RAY, P. (2000). *Microhyla sholigari*, a new species of microhylid frog (Anura: Microhylidae) from Karnataka, India. *Hamadryad*, 25, 38–44.
- FRANK, N. & RAMUS, E. (1995). Complete Guide to Scientific and Common Names of Amphibians and Reptiles of the World. Pottsville, Pennsylvania, NG Publishing Inc.
- FERNANDO, P. & SIRIWARDHANE, M. (1996). Microhyla karunaratnei (Anura: Microhylidae), a new species of frog endemic to Sri Lanka. Journal of South Asian Natural History, 2, 135–142.
- FROST, D. R. (2004). Amphibian species of the world: an online reference. Version 4.0 (August 2006). Available at: http://research. amnh.org/herpetology/amphibia/index.php.
- FROST, D. R. (2018). Amphibian species of the world: an online reference. Version 6.0 (Accessed on 01 March 2018). Available at: http://research.amnh.org/herpetology/amphibia/index.html.
- GARG, S. & BIJU, S. D. (2017). Description of four new species of Burrowing Frogs in the *Fejervarya rufescens* complex (Dicroglossidae) with notes on morphological affinities of *Fejervarya* species in the Western Ghats. *Zootaxa*, 4277, 451–490.
- GARG, S., SUYESH, R., SUKESHAN, S. & BIJU, S. D. (2017). Seven new species of Night Frogs (Anura, Nyctibatrachidae) from the Western Ghats Biodiversity Hotspot of India, with remarkably high diversity of diminutive forms. *PeerJ*, 5, e3007.
- GARG, S., DAS, A., KAMEI, R. G. & BIJU, S. D. (2018A). Delineating *Microhyla ornata* (Anura, Microhylidae): Mitochondrial DNA barcodes resolve century-old taxonomic misidentification. *Mitochondrial DNA Part B*, **3**, 856–861.
- GARG, S., SENEVIRATHNE, G., WIJAYATHILAKA, N., PHUGE, S., DEUTI, K., MANAMENDRA-ARACHCHI, K., MEEGASKUMBURA, M. & BIJU, S. D. (2018B). An integrative taxonomic review of the South Asian microhylid genus Uperodon. Zootaxa, 4384, 001–088.
- GROSSELT, O., SENGUPTA, S., GUPTA, A., VAUCHE, M. & GUPTA, S. (2005). *Microhyla heymonsi* Vogt, 1911 (Anura: Microhylidae) from mainland India, with bioacoustic analysis of its advertising call. *Hamadryad*, 29, 131–133.
- GUIBÉ, J. (1950 "1948"). Catalogue des Types d'Amphibiens du Muséum National d'Histoire Naturelle. Paris, Imprimerie Nationale.
- GUNTHER, A. C. L. G. (1859 "1858"). Catalogue of the Batrachia Salientia in the Collection of the British Museum. London, Taylor and Francis.
- HARIKRISHNAN, S., CHANDRAMOULI, S. & VASUDEVAN, K. (2012). A survey of herpetofauna on Long Island, Andaman and Nicobar Islands, India. *Herpetological Bulletin*, **119**, 19–28.
- Hasan, M., Islam, M. M., Khan, M. M. R., Alam, M. S., Kurabayashi, A., Igawa, T., Kuramoto, M. & Sumida, M. (2012).

Cryptic anuran biodiversity in Bangladesh revealed by mitochondrial 16S rRNA gene sequences. *Zoological Science*, **29**, 162–172.

- HASAN, M., ISLAM, M.M., KURAMOTO, M., KURABAYASHI, A. & SU-MIDA, M. (2014A). Description of two new species of *Microhyla* (Anura: Microhylidae) from Bangladesh. *Zootaxa*, 3755, 401–418.
- HASAN, M., ISLAM. M. M., KHAN, M. R., IGAWA, T., ALAM, M. S., DJONG, H. T., KURNIAWAN, N., JOSHY, H., SEN, Y.H., BELABUT, D. M., KURABAYASHI, A., KURAMOTO, A. & SUMIDA, M. (2014B). Genetic divergences of South and Southeast Asian frogs: a case study of several taxa based on 16S ribosomal RNA gene data with notes on the generic name *Fejervarya*. *Turkish Journal of Zoology*, **38**, 389–411.
- HEYER, W. R. (1971). Mating calls of some frogs from Thailand. *Fieldiana Zoology*, 58, 61–82.
- HOWLADER, M. S. A., NAIR, A., GOPALAN, S. V. & MERILÄ, J. (2015). A new species of *Microhyla* (Anura: Microhylidae) from Nilphamari, Bangladesh. *PLoS ONE*, **10**, e0119825.
- HOWLADER, M. S. A., NAIR, A. & MERILÄ, J. (2016). A new species of frog (Anura: Dicroglossidae) discovered from the mega city of Dhaka. *PLoS ONE*, **11**, e0149597.
- JANG-LIAW, N. H. & CHOU, W. H. (2015). Anuran fauna of Taiwan and adjacent islands based on valid specimen records. *Collection and Research*, 28, 5–53.
- JERDON, T. C. (1854 "1853"). Catalogue of reptiles inhabiting the Peninsula of India. *Journal of the Asiatic Society of Bengal*, 22, 522-534.
- JERDON, T. C. (1870). Notes on Indian herpetology. Proceedings of the Asiatic Society of Bengal, 1870, 66–85.
- KHATIWADA, J. R., SHU, G. C., WANG, S. H., THAPA, A., WANG, B. & JIANG, J. P. (2017). A new species of the genus *Microhyla* (Anura: Microhylidae) from Eastern Nepal. *Zootaxa*, **4254**, 221–239.
- LALREMSANGA, H. T., SAILO, S. & HOOROO, R. N. K. (2007). Geographic distribution: *Microhyla butleri*. Herpetological Review, 38, 348–349.
- LIBRADO, P. & ROZAS, J. (2009). DnaSP v5: A software for comprehensive analysis of DNA polymorphism data. *Bioinformatics*, 25, 1451–1452.
- LYNCH, J. D. (1971). Evolutionary relationships, osteology, and zoogeography of leptodactyloid frog. Lawrence, University of Kansas Publications, Museum of Natural History.
- MAHONY, S., HASAN, M. K., KABIR, M. M., AHMED, M. & HOSSAIN, M. K. (2009). A catalogue of amphibians and reptiles in the collection of Jahangirnargar University, Dhaka, Bangladesh. *Hamadryad*, 34, 80–94.
- MANTHEY, U. & GROSSMANN, W. (1997). Amphibien & Reptilien Südostasiens. Münster, Natur und Tier.
- MATHEW, R. & SEN, N. (2010). Pictorial Guide to Amphibians of North East India. Kolkata, Zoological Survey of India.
- MATSUI, M. (2011). Taxonomic revision of one of the Old World's smallest frogs, with description of a new Bornean *Microhyla* (Amphibia, Microhylidae). *Zootaxa*, 2814, 33–49.
- MATSUI, M., ITO, H., SHIMADA, T., OTA. H., SAIDAPUR, S. K., KHON-SUE, W., TANAKA-UENO, T. & WU, G. F. (2005). Taxonomic relationships within the Pan-Oriental narrow-mouth toad *Microhyla ornata* as revealed by mtDNA analysis (Amphibia, Anura, Microhylidae). *Zoological Science*, **22**, 489–495.
- MATSUI, M., HAMIDY, A., BELABUT, D. M., AHMAD, N., PANHA, S., SUDIN, A., KHONSUE, W., OH, H. S., YONG, H. S., JIANG, J. P. & NISHIKAWA, K. (2011). Systematic relationships of Oriental tiny frogs of the family Microhylidae (Amphibia, Anura) as revealed by mtDNA genealogy. *Molecular Phylogenetics and Evolution*, 61, 167–176.
- MATSUI, M., HAMIDY, A. & ETO, K. (2013). Description of a new species of *Microhyla* from Bali, Indonesia (Amphibia, Anura). *Zootaxa*, 3670, 579–590.
- MYERS, C. W. & DUELLMAN, W. E. (1982). A New Species of *Hyla* from Cerro Colorado, and other Tree frog records and geographical notes from Western Panama. *American Museum novitates*, 2752, 1–32.

- PARKER, H. W. (1927). A revision of the frogs of the genera Pseudopaludicola, Physalaemus, and Pleurodema. Journal of Natural History, 20, 450–478.
- PARKER, H. W. (1934). A Monograph of the Frogs of the Family Microhylidae. London, Trustees of the British Museum.
- PARKER, H. W. & OSMAN-HILL, W. C. (1949 "1948"). Frogs of the genus Microhyla from Ceylon. Annals and Magazine of Natural History, 12, 759–764.
- PELOSO, P. L. V., FROST, D. R., RICHARDS, S. J., RODRIGUES, M. T., DONNELLAN, S. C., MATSUI, M., RAXWORTHY, C. J., BIJU, S. D., LEMMON, E. M., LEMMON, A. R. & WHEELER, W. C. (2016). The impact of anchored phylogenomics and taxon sampling on phylogenetic inference in Narrow-mouthed Frogs (Anura, Microhylidae). *Cladistics*, **32**, 113–140.
- PILLAI, R. S. (1977). On two frogs of the family Microhylidae from Andamans including a new species. *Proceedings of the Indian Academy of Sciences*, 86, 135–138.
- POSADA, D. & CRANDALL, K. A. (1998). MODELTEST: testing the model of DNA substitution. *Bioinformatics*, 14, 817–818.
- POYARKOV JR, N. A., VASSILIEVA, A. B., ORLOV, N. L., GALOYAN, E. A., DAO, T. T. A., LE, D. T. T., KRETOVA, V. D. & GEISSLER, P. (2014). Taxonomy and distribution of narrow-mouth frogs of the genus *Microhyla* Tschudi, 1838 (Anura: Microhylidae) from Vietnam with descriptions of five new species. *Russian Journal of Herpetology*, **21**, 89–148.
- RONQUIST, F. & HUELSENBECK, J. P. (2003). MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19, 1572–1574.
- SARKAR, A. K. (1990). Taxonomic and ecological studies on the Amphibians of Andaman and Nicobar Islands, India. *Records* of *Zoological Survey of India*, 86, 103–117.
- SAVAGE, J. M. & HEYER, W. R. (1967). Variation and distribution in the tree-frog genus *Phyllomedusa* in Costa Rica, Central America: With 6 figures. *Studies on Neotropical Fauna and Environment*, 5, 111–131.
- SCLATER, W. L. (1892). *List of the Batrachia in the Indian Museum*. London, Taylor and Francis.
- SESHADRI, K. S., SINGAL, R., PRITI, H., RAVIKANTH, G., VIDISHA, M. K., SAURABH, S., PRATIK, M. & GURURAJA, K. V. (2016A). *Microhyla laterite* sp. nov., a new species of *Microhyla* Tschudi, 1838 (Amphibia: Anura: Microhylidae) from a laterite rock formation in South West India. *PLoS ONE*, **11**, e0149727.
- SESHADRI, K. S., PRITI, H., RAVIKANTH, G., VIDISHA, M. K., VINEETH, K. K., SINGAL, R., SARMA, R. R., ARAVIND, N. A. & GURURAJA, K. V. (2016B). Redescription and Range Extension of *Microhyla sholigari* Dutta & Ray (Amphibia: Anura: Microhylidae) from South West India. *Zootaxa*, **4208**, 547–560.
- SHERIDAN, J. A., BICKFORD, D. & SU, K. F. Y. (2010). An examination of call and genetic variation in three wide-ranging Southeast Asian anuran species. *Raffles Bulletin of Zoology*, 58, 369–379.
- SILVESTRO, D. & MICHALAK, I. (2012). raxmlGUI: a graphical frontend for RAxML. Organisms Diversity & Evolution, 12, 335– 337.
- SIMON, C., FRATI, F., BECKENBACH, A., CRESPI, B., LIU, H. & FLOOK, P. (1994). Evolution, weighting and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America*, 87, 651–701.
- STAMATAKIS, A., HOOVER, P., ROUGEMONT, J. & RENNER, S. (2008). A rapid bootstrap algorithm for the RAXML Web Servers. Systematic Biology, 57, 758–771.
- STEPHENS, M., SMITH, N. J. & DONNELLY, P. (2001). A new statistical method for haplotype reconstruction from population data. *The American Journal of Human Genetics*, 68, 978–989.
- STOLICZKA, F. (1870). Observations on some Indian and Malayan Amphibia and Reptilia. *Journal of the Asiatic Society of Ben*gal, 39, 134–157.
- SWOFFORD, D. L. (2002). PAUP\*: Phylogenetic Analysis Using Parsimony (\* and other methods). Version 4.0b10. Sunderland, Massachusetts: Sinauer Association Inc.

- TAMURA, K., STECHER, G., PETERSON, D., FILIPSKI, A. & KUMAR, S. (2013). MEGA6: Molecular Evolutionary Genetics Analysis Version 6.0. *Molecular Biology and Evolution*, 30, 2725–2729.
- TAYLOR, E. H. (1934). Zoological results of the third De Schauensee Siamese Expedition, Part III. Amphibians and reptiles. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 86, 281–310.
- TAYLOR, E. H. (1962). The amphibian fauna of Thailand. University of Kansas Science Bulletin, 43, 265–599.
- TAYLOR, W. R. & VAN DYKE, G. C. (1985). Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium*, 9, 107–119.
- THEOBALD, W. (1873). Note regarding certain type specimens of Batrachia in the Asiatic society's Museum. *Proceedings of the Asiatic Society of Bengal*, **1873**, 110–112.
- VAN BOCXLAER, I., ROELANTS, K., BIJU, S. D., NAGARAJU, J. & BOS-SUYT, F. (2006). Late Cretaceous vicariance in Gondwanan amphibians. *PLoS One*, 1, e74.
- VAN DER MEIJDEN, A., VENCES, M., HOEGG, S., BOISTEL, R., CHAN-NING, A. & MEYER, A. (2007). Nuclear gene phylogeny of narrow-mouthed toads (Family: Microhylidae) and a discussion of competing hypotheses concerning their biogeographical origins. *Molecular Phylogenetics and Evolution*, 44, 1017–1030.
- VINEETH, K. K., RADHAKRISHNA, U. K., GODWIN, R. D., SAHA, A., PA-TIL, R. K. & ARAVIND, N. A. (2018). A new species of *Microhyla* Tschudi, 1838 (Anura: Microhylidae) from West Coast of India: an integrative taxonomic approach. *Zootaxa*, **4420**, 151–179.
- Appendix

File S1. List of morphologically studied specimens.

Microhyla achatina. INDONESIA: Java, Bogor, UIMZ 0031-0035 and UIMZ 0035b, six adult males. Microhyla kodial. INDIA: Karnataka state, Mangaluru city, Baikampady, SDBDU 2017.3673-3676 and SDBDU 2017.3687-3689, seven adult males. Microhyla orientalis. INDONESIA: Bali, Wongaya Gede, UIMZ 0037-0041 and UIMZ 0041b, six adult males. Microhyla heymonsi. CHINA: "Formosa" [=Taiwan], ZMB 55182 and ZMB 23334, syntypes, two adult males; Taiwan Province, CIB 65579-65580 and CIB 65582-65583, four adult males. Microhyla cf. heymonsi. INDIA: Andaman Islands, WII-HS08, an adult male. Microhyla berdmorei. MYANMAR: "Arakan", ZSI 9718-9720; INDIA: Assam state, Amchang, ADA 45, an adult male; Assam state, Barail, ADA 5227-5228 and ADA 5243, three adult males; Meghalaya state, Nongkhellyam WLS, A0949 and A0951, two adult males. Microhyla pulchra. CHINA: Guangdong Province, Guangzhou City, CIB 68624, an adult male; Guizhou Province, Anlong, CIB 68812, an adult male; Hunan Province, Yizhang, CIB 68886, an adult male; Yunnan Province, He Kou, CIB 103704, an adult female. Microhyla chakrapanii. INDIA: "Mayabunder (east of Burma temple), North Andamans", ZSI-SRS VA/770, holotype, an adult male; Andaman Islands, WII-HC010, WII-HC095, WII-HC112, WII-HC184, and WII-HC185, five adult males. Microhyla fissipes. CHINA: Taiwan Province, Taiwan City, CIB 68500, an adult male; Fujian Province, Chong'an, CIB 67519, CIB 67525, CIB 67535, and CIB 67540, four adult males; Microhyla mixtura. CHINA: Sichuan Province, Wanyuan Country, CIB 65691-65692, CIB 65696, CIB 65701,

- VOGT, T. (1911). Beitrag zur Amphibienfauna der Insel Formosa. Sitzungsberichte der Gesellschaft Naturforschender Freunde, 1911, 179–184.
- WIJAYATHILAKA, N. & MEEGASKUMBURA, M. (2016). An acoustic analysis of the genus *Microhyla* (Anura: Microhylidae) of Sri Lanka. *PLoS One*, **11**, e0159003.
- WIJAYATHILAKA, N., GARG, S., SENEVIRATHNE, G., KARUNARATHNA, N., BIJU, S. D. & MEEGASKUMBURA, M. (2016). A new species of *Microhyla* (Anura: Microhylidae) from Sri Lanka: an integrative taxonomic approach. *Zootaxa*, **4066**, 331–342.
- WOGAN, G. O. U., VINDUM, J. V., WILKINSON, J. A., KOO, M. S., SLO-WINSKI, J. B., WIN, H., THIN, T., KYI, S. W., OO, S. L., LWIN, K. S. & SHEIN, A. K. (2008). New country records and range extensions for Myanmar amphibians and reptiles. *Hamadryad*, 33, 83–96.
- YUAN, Z.Y., SUWANNAPOOM, C., YAN, F., POYARKOV JR, N. A, NGUY-EN, S. N., CHEN, H. M., CHOMDEJ, S., MURPHY, R. W. & CHE, J. (2016). Red river barrier and Pleistocene climatic fluctuations shaped the genetic structure of *Microhyla fissipes* complex (Anura: Microhylidae) in southern China and Indochina. *Current Zoology*, **62**, 531–543.

and CIB 65706, five adult males; Microhyla mukhlesuri. INDIA: Mizoram state, SDBDU 2010.20-21, SDBDU 2010.132b, and SDBDU 2010.1333, four adult males. Microhyla mymensinghensis. INDIA: Assam state, Barail, ADA 50 and ADB50B, two adult males; Tripura state, Sepahijala WLS, SDBDU 2009.445, an adult male; Tripura state, Trishna WLS, SDBDU 2009.482, an adult male; Tripura state, Trishna WLS, SDBDU 2009.541, an adult male; Tripura state, Jampui Hills, SDBDU 2009.610, an adult male. Microhyla nilphamariensis. INDIA: Chhattisgarh, Durga Dhara Falls, SDBDU 2011.586, an adult male; Karnataka state, Manipal, SDBDU 2015.3060, an adult male; Maharashtra state, Amboli, SDBDU 2014.2482, an adult male; Maharashtra state, Koyna, SDBDU 2010.349, an adult male; Odisha state, Khurda, an adult male; Uttarakhand state, Tuntowala, ADM 017, an adult male. Microhyla ornata. INDIA: "côte Malabar", MNHNP 5035, holotype, an adult male; Karnataka state, Bannerghatta, SDBDU 2014.2555-2557, three adult males; Karnataka state, BR Hills, SDBDU 2014.2539, an adult male; Karnataka state, Sakleshpur, SDBDU 2012.2198, an adult male. SRI LANKA: Anuradhapura, DZ 1052, an adult male; Anuradhapura, DZ 1471, an adult male; Kumbalagama, DZ 1085, an adult male; Puttalam, DZ 1104, an adult male; Maakandura, DZ 1432, an adult male. Microhyla mihintalei. SRI LANKA: Anuradhapura, DZ 1553, holotype, an adult male; Anuradhapura, DZ 1554-1557, paratypes, four adult males; Anuradhapura, DZ 1467-1468 and DZ 1473, paratypes, three adult males; Maakandura, DZ 1410, an adult male. Microhyla ru*bra.* INDIA: Karnataka state, Bannerghatta, ZSI/WGRC/V/A/960, neotype, an adult male; Karnataka state, Bannerghatta, SDBDU 2014.2558, SDBDU 2014.2560–2561, three adult males; Karnataka state, BR Hills, SDBDU 2014.2548, an adult male; Karnataka state, Shimoga, SDBDU 40132–40134, three adult males. *Microhyla darreli sp.* nov. INDIA: Kerala state, Karamana, ZSI/WGRC/V/A/961, holotype, an adult male; Kerala state, Karamana, ZSI/WGRC/V/A/962–965, paratypes, four adult males; Kerala state, Karamana, SDBDU 2015.2976, an adult male; Kerala state, Chathankodu, SDBDU 2009.101, an adult male. *Microhyla karunaratnei*. SRI LANKA: Rathnapura, Morningside, DZ 1529–DZ 1531, three adult males. *Microhyla laterite*. INDIA: Karnataka

state, "Herga village, Manipal", BNHS 5964, holotype, an adult male; Karnataka state, Manipal, SDBDU 2015.3062–3064 and SDBDU 2015.3066–3067, five adult males. *Microhyla sholigari*. INDIA: Karnataka state, "Bhargavi stream bed near Doddasampige", Biligirirangan Hills, ZSIC A9061, holotype, a subadult female; Karnataka state, BR Hills, SDBDU 2014.2533 and SDBDU 2014.2537, two adult males; Karnataka state, BR Hills, SDBDU 2014.2533 and SDBDU 2016.3442–3444, three adult males. *Microhyla zeylanica*. SRI LANKA: "Bopats" (Bopatalawa), BMNH 1948.1.1.3, holotype, an adult male; Horton Plains National Park, DZ 1419–1421, three adult males.

#### File S2. Vocalization in four closely related *Microhyla* species from East and Southeast Asia

*Microhyla achatina*. The calls of *Microhyla achatina* (voucher UIMZ 0031) were recorded at Bogor, Java on 4 October 2017, between 20:30–21:00 h, at air temperature:  $28^{\circ}$ C dry bulb,  $27^{\circ}$ C wet bulb. The male produced a single type of call with pulsatile temporal structure. Calls were not delivered in groups and showed uniform intervals. The call duration was 228.6 ms (116.2–285.3 ms) with 8 pulses (4–9 pulses) delivered at a rate of 26.4 pulses/s (25.6–28.5 pulses/s), rise time of 103.2 ms (38.4–122.3 ms), and fall time of 109.6 ms (40.2–163.2 ms). The call spectrum was characterized by single broad peak with the overall dominant frequency of 3.3 kHz (3.2–3.4 kHz) (Fig. 6; Table S4).

*Microhyla orientalis.* The calls of *Microhyla orientalis* (voucher UIMZ 0037) were recorded at Wongaya Gede, Bali, on 2 October 2017, between 19:30–20:00 h, at air temperature:  $25.2^{\circ}$ C dry bulb, 24.0°C wet bulb. The male produced a single type of call with pulsatile temporal structure. Calls were not delivered in groups and showed uniform intervals. The mean call duration was 62.0 ms (48.2–67.4 ms) with 5 pulses (3–5 pulses) delivered at a rate of 57.7 pulses/s (46.5–64.5 pulses/s), rise time of 22.6 ms (22.1–23.2 ms), and fall time of 39.6 ms (26.2–44.1 ms). The call spectrum was characterized by single broad peak with the overall dominant frequency of 3.7 kHz (Fig. 6; Table S4).

*Microhyla fissipes.* The calls of *Microhyla fissipes* (voucher CIB HN034) were recorded at Chengmai, Hainan Island, by Yulong Li, on 29 May 2016, between 20:00–24:00 h, at air temperature: 26.5°C

dry bulb, 24.5°C wet bulb. The male was observed to produce a single type of call with pulsatile temporal structure and the calls were not delivered in groups. The mean call duration was 236.2 ms (229.2–251.3 ms) with 15 pulses (15–16 pulses) delivered at a rate of 61.8 pulses/s (61.4-62.5 pulses/s), rise time of 149.2 ms (130.2-163.3 ms), and fall time of 87.6 ms (69.2-104.4 ms). The call spectrum was characterized by two broad peaks with mean dominant frequency of 3.0 kHz (Fig. 13; Table S4). Further, our calls of *Microhyla fissipes* recorded from China were largely similar to *M. fissipes* calls published by HEYER (1971) as '*M. ornata'* in duration 230–250 ms (vs. 230–310 ms) and pulse rate 61.0-61.5 pulses/s (vs. 53.0–63.0 pulses/s) (Table S4).

*Microhyla palmipes.* The calls of *Microhyla palmipes* were recorded at Telaga Warna, Java, on 26 October 2017, between 23:00-23:30 h. The male produced a single type of call with pulsatile temporal structure. Unlike other microhylids in the current study, calls were delivered in groups with uniform intervals. The mean call duration was 109.6 ms (58.2–164.4 ms) with 11 pulses (6–13 pulses) delivered at a rate of 79.8 pulses/s (73.5–90.9 pulses/s), rise time of 33.2 ms (20.1–45.2 ms), and fall time of 67.2 ms (38.2–105.1 ms). The call spectrum was characterized by single broad peak with the overall dominant frequency of 3.5 kHz (3.4–3.5 kHz) (Fig. 25; Table S4).

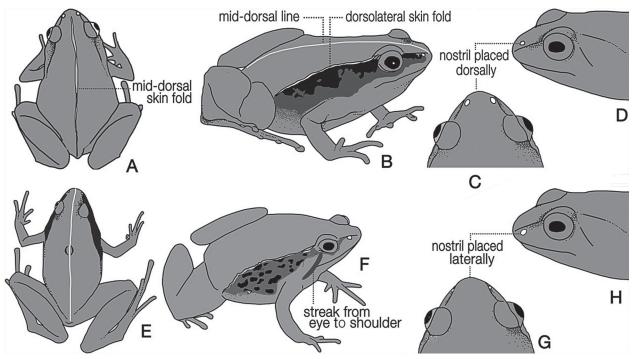


Fig. S1. Graphic scheme for meristic characters used in the study. A. Mid-dorsal skin fold. B. Mid-dorsal line, dorsolateral skin fold with lateral marking or band. C-D. Nostril placed dorsally. E. Mid-dorsal line and '()' marking. F. Streak from posterior corner of eye to shoulder. G-H. Nostril placed laterally.

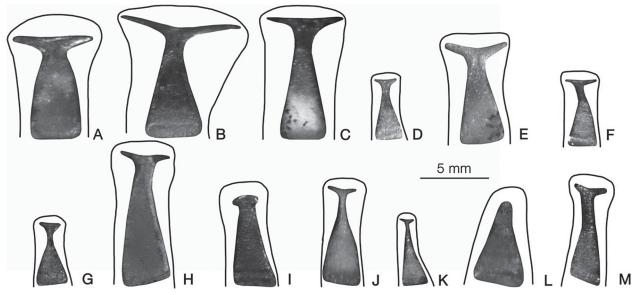


Fig. S2. Terminal phalanges of toe IV in *Microhyla* species. A. M. achatina. B. M. berdmorei. C. M. chakrapanii. D. M. darreli sp. nov. E. M. cf. heymonsi. F. M. kodial. G. M. laterite. H. M. mukhlesuri. I. M. mymensinghensis. J. M. nilphamariensis. K. M. ornata. L. M. rubra. M. M. sholigari.

	Species	Locality	Voucher No.	Accession No.
1	Microhyla achatina	Indonesia: Java, Ungaran	MZB Amp 16402	AB634656
2	Microhyla achatina	Indonesia: Java, Gede Pangrango	MDK:24	AB634657
3	Microhyla achatina	Indonesia: Java, Ungaran	MZBAmp 16401	AB598335
4	Microhyla achatina	Indonesia, Java Island	RMB2629	KC822492
5	Microhyla achatina	Indonesia: Java, Ungaran	MZBAmp16402	KM509162
6	Microhyla "sp. 3"	Indonesia: Sumatra, Lampung	MZB Amp 15291	AB634680
7	Microhyla "sp. 3"	Indonesia: Sumatra, Bengkulu	MZB Amp 16328	AB634681
8	Microhyla annectens	Malaysia: Selangor, Genting	KUHE 53373	AB634658
9	Microhyla berdmorei	Malaysia: Selangor, Gombak	KUHE 52034	AB598338
10	Microhyla berdmorei	India: Tripura, Gumti WLS	SDBDU 2009.567	MH807384
11	Microhyla berdmorei	India: Tripura, Vanghmun, Jampui Hills	SDBDU 2009.609	MH807385
12	Microhyla berdmorei	India: Tripura, Sepahijala WLS	SDBDU 2009.440	MH807386
13	Microhyla berdmorei	India: Tripura, Trishna WLS	SDBDU 2009.509	MH807387
14	Microhyla berdmorei	India: Assam, Tellachera, Near Marua	WII 5676	MH807388
15	Microhyla berdmorei	Bangladesh: Sylhet, Golapganj	Haplotype: Msp-Bd1	AB530540
16	Microhyla berdmorei	Bangladesh: Sylhet, Golapganj & Bandarban	Haplotype: Msp-Bd2	AB530541
17	Microhyla berdmorei	Bangladesh: Sylhet, Golapganj & Dandarban Bangladesh: Sylhet, Golapganj	Haplotype: Msp-Bd2 Haplotype: Msp-Bd3	AB530542
18	Microhyla berdmorei	Malaysia: Gombak FSC	Haplotype: Msp-Bd5	AB530638
19	Microhyla berdmorei	Indonesia: Sumatra, Bengkulu	MZB Amp 16413	AB634660
20	Microhyla berdmorei	Indonesia: Kalimantan, Paramasan	MZB Amp 10413 MZB Amp 15270	AB634661
20	Microhyla berdmorei	Malaysia: Terengganu, Besut	KUHE:52373	AB634662
21	Microhyla berdmorei	Thailand: Phrae, Mae Yom	KUHE:21992	
22	Micronyla beramorei		KURE:21992	AB634667
23	Microhyla berdmorei	Myanmar: Sagaing, Alaungdaw Kathapa Natio- nal Park	CAS:HERP:204876	KC179981
24	Microhyla berdmorei	Malaysia, Perlis, 9 km W Padang Besar, FRIM field station	JAM1995	KC822491
25	Microhyla berdmorei	Thailand: Phang Nga, Phang-nga Breeding Station	TAD_P917	KR827906
26	Microhyla berdmorei	Laos: Luang Prabang, Kouangxi Waterfall	K1463	KR827907
27	Microhyla berdmorei	Thailand: Chiang Mai, Doi Chiang Dao	K3008	KR827908
28	Microhyla berdmorei	Laos: Phongsaly, Ha Tinh	2005.0169	KR827909
29	Microhyla berdmorei	Laos: Luang Prabang, Ban Dong Khan	2006.2330	KR827910
30	Microhyla berdmorei	Cambodia: Siem Reap	SGK4982	KU840572
31	Microhyla cf. berdmorei	Myanmar: Magway, Pakoku	CAS:HERP:215851	KM509166
32	Microhyla borneensis	Malaysia: Sarawak, Gunung Serapi	KUHE 53165	AB598329
33	Microhyla borneensis	Malaysia: Sarawak, Gunung Serapi	KUHE:53020	AB598327
34	Microhyla borneensis	Malaysia: Sarawak, Gunung Serapi	KUHE:53033	AB598328
35	Microhyla borneensis	Malaysia: Sarawak, Gunung Serapi	SM:081126	AB598330
36	Microhyla borneensis	Malaysia: Sarawak, Gunung Serapi	KUHE NNL M13	AB598331
37	Microhyla borneensis	Malaysia: Sarawak, Gunung Serapi	KUHE NNL M14	AB598332
38	Microhyla borneensis	Malaysia: Sarawak, Serapi	KUHE:53938	AB634663
39	Microhyla borneensis	Malaysia	VUB0588	EF017951
40	Microhyla borneensis	Malaysia: Sarawak, Kubah National Park	ZMH A10019	GU154881
41	Microhyla borneensis	Malaysia: Sarawak, Kubah National Park	ZRC 1.12432	GU154885
42	Microhyla borneensis	Malaysia: Sarawak, Kubah National Park	ZRC 1.12441	GU154886
43	Microhyla borneensis	NA	KNP22	KT851977
44	Microhyla borneensis	NA	KNP1134	KT851979
45	Microhyla borneensis	NA	KNP1096	KT851982
46	Microhyla borneensis	NA	KNP1034	KT851983
47	Microhyla butleri	Vietnam: A Roang, A Luoi	KUHE 40591	AB634664
48	Microhyla chakrapanii	India: Andaman Islands	Not preserved	MH807389
49	Microhyla darreli <b>sp. nov.</b>	India: Thiruvananthapuram, Karamana	ZSI/WGRC/V/A/962	MH807390
49 50	Microhyla fissipes	China: Anhui, Huangshan	KUHE 32943	AB201185
51	Microhyla fissipes	NA	NA	DQ512876
51		NA NA	NA	NC009422
52	Microhyla fissipes			

Table S1. List of samples used for the molecular study.

54	Microhyla heymonsi	NA	NA	AY458596
55	Microhyla heymonsi	NA	NA	NC006406
56	Microhyla heymonsi	China: Sichuan, Zihuai	061002	KU840570
57	Microhyla heymonsi	NA	NA	AF215372
58	Microhyla heymonsi	NA	NA	AF285200
59	Microhyla heymonsi	NA	NA	AF285200
		Vietnam: Ha Giang, Yen Minh, Du Gia Commu-		
60	Microhyla heymonsi	ne, Khau Ria Village	AMNH A163850	DQ283382
61	Microhyla heymonsi	Vietnam: Vinh Phuc, Tam Dao	K739	KR827935
62	Microhyla 'heymonsi'	Thailand	KU: field tag DSM 1136	HM359087
63	Microhyla 'heymonsi'	Thailand	KU: field tag DSM 1152	HM359088
64	Microhyla 'heymonsi'	Thailand	KU:field tag DSM 1153	HM359089
65	Microhyla 'heymonsi'	Thailand	KU:field tag DSM 1205	HM359090
66	Microhyla 'heymonsi'	Laos: Luang Prabang, Luang Prabang	1997.8354	KR827932
67	Microhyla 'heymonsi'	Laos: Viangchan, Vientiane	1999.6069	KR827934
68	Microhyla 'heymonsi'	Thailand: Bangkok, Kasetsart University	0974Y2	KR827937
69	Microhyla 'heymonsi'	Thailand: Bangkok, Kasetsart University	0974Y1	KR827938
70	Microhyla 'heymonsi'	Thailand: Chiang Mai, Doi Chiang Dao	K3066	KR827940
71	Microhyla 'heymonsi'	Laos: Luang Prabang, Ban Nong Di	2006.2341	KR827943
72	Microhyla 'heymonsi'	Laos: Luang Prabang, Ban Keng Koung	2006.2337	KR827944
73	Microhyla 'heymonsi'	Laos: Phongsali, Long Nai Khao	2004.0414	KR827933
74	Microhyla 'heymonsi'	Laos: Luang Prabang, Ban Sop Choun	2006.2346	KR827936
75	Microhyla 'heymonsi'	Laos: Luang Prabang, Ban Sop Khao	2006.2343	KR827941
76	Microhyla 'heymonsi'	Laos: Luang Prabang, Ban Vang Thong	2006.2348	KR827942
77	Microhyla 'heymonsi'	Thailand: Phang Nga, Sa Nang Manora Forest Park	TAD_P329	KR827939
78	Microhyla 'heymonsi'	Myanmar: Hlawgaw Wildlife Park, Yangon	CAS:HERP:210748	KC179993
79	Microhyla 'heymonsi'	Thailand: Ranong, Ranong spa	KUHE:23856	AB598336
80	Microhyla 'heymonsi'	Thailand: Kanchanaburi, Thong Pha Phum	KUHEK1845	AB201190
81	Microhyla 'heymonsi'	Malaysia: University Malay Campus	Haplotype: Mhey-My1	AB530636
82	Microhyla 'heymonsi'	Malaysia: University Malay Campus	Haplotype: Mhey-My2	AB530637
83	Microhyla 'heymonsi'	Singapore	RM MIHEJS2	HM359091
84	Microhyla 'heymonsi'	Singapore	RM MIHEJS3	HM359092
85	Microhyla 'heymonsi'	Singapore	RM MIHEJS4	HM359093
86	Microhyla 'heymonsi'	Singapore	RM MIHEJS5	HM359094
87	Microhyla 'heymonsi'	Singapore	RM MIHEJS6	HM359095
88	Microhyla 'heymonsi'	Singapore	RM MIHEJS8	HM359096
89	Microhyla cf. heymonsi	India: Andaman Islands	Not preserved	MH807391
90	Microhyla karunaratnei	Sri Lanka: Morningside, Sinharaja	DZ 1529	MH807392
			DZ 1529	MH807393
91	$Nucronvla karunaramoi$	Sri Lanka: Morningside Sinharaia		
91 92	Microhyla karunaratnei Microhyla kodial	Sri Lanka: Morningside, Sinharaja	SDBDU 2017 3674	
92	Microhyla kodial	India: Karnataka, Mangalore	SDBDU 2017.3674 BNHS 5965	MH807394
92 93	Microhyla kodial Microhyla laterite	India: Karnataka, Mangalore India: Karnataka, Manipal	BNHS 5965	MH807394 KT600670
92 93 94	Microhyla kodial Microhyla laterite Microhyla laterite	India: Karnataka, Mangalore India: Karnataka, Manipal India: Karnataka, Manipal	BNHS 5965 GL3302	MH807394 KT600670 KT600671
92 93 94 95	Microhyla kodial Microhyla laterite Microhyla laterite Microhyla laterite	India: Karnataka, MangaloreIndia: Karnataka, ManipalIndia: Karnataka, ManipalIndia: Karnataka, Mangalore	BNHS 5965 GL3302 SDBDU 2015.3062	MH807394 KT600670 KT600671 MH807395
92 93 94 95 96	Microhyla kodial Microhyla laterite Microhyla laterite Microhyla laterite Microhyla laterite	India: Karnataka, Mangalore         India: Karnataka, Manipal         India: Karnataka, Manipal         India: Karnataka, Mangalore         India: Karnataka, Mangalore         India: Kerala, Kannur, Madayipara	BNHS 5965 GL3302 SDBDU 2015.3062 SDBDU 2017.3583	MH807394 KT600670 KT600671 MH807395 MH807396
92 93 94 95 96 97	Microhyla kodial Microhyla laterite Microhyla laterite Microhyla laterite Microhyla laterite Microhyla laterite	India: Karnataka, MangaloreIndia: Karnataka, ManipalIndia: Karnataka, ManipalIndia: Karnataka, MangaloreIndia: Kerala, Kannur, MadayiparaIndia: Kerala, Kannur, Madayipara	BNHS 5965 GL3302 SDBDU 2015.3062 SDBDU 2017.3583 SDBDU 2017.3696	MH807394 KT600670 KT600671 MH807395 MH807396 MH807397
92 93 94 95 96 97 98	Microhyla kodial Microhyla laterite Microhyla laterite Microhyla laterite Microhyla laterite Microhyla laterite Microhyla laterite	India: Karnataka, Mangalore         India: Karnataka, Manipal         India: Karnataka, Manipal         India: Karnataka, Mangalore         India: Karnataka, Mangalore         India: Kerala, Kannur, Madayipara         India: Kerala, Kannur, Madayipara         India: Kerala, Kasargod, Anakallu	BNHS 5965 GL3302 SDBDU 2015.3062 SDBDU 2017.3583 SDBDU 2017.3696 SDBDU 2017.3602	MH807394 KT600670 KT600671 MH807395 MH807396 MH807397 MH807398
92 93 94 95 96 97 98 99	Microhyla kodial Microhyla laterite Microhyla laterite Microhyla laterite Microhyla laterite Microhyla laterite Microhyla laterite Microhyla malang	India: Karnataka, Mangalore         India: Karnataka, Manipal         India: Karnataka, Manipal         India: Karnataka, Mangalore         India: Karnataka, Mangalore         India: Kerala, Kannur, Madayipara         India: Kerala, Kannur, Madayipara         India: Kerala, Kasargod, Anakallu         Malaysia: Sarawak, Gunung Serapi	BNHS 5965 GL3302 SDBDU 2015.3062 SDBDU 2017.3583 SDBDU 2017.3696 SDBDU 2017.3602 KUHE 53018	MH807394 KT600670 KT600671 MH807395 MH807396 MH807397 MH807398 AB598319
92 93 94 95 96 97 98 98 99 100	Microhyla kodial Microhyla laterite Microhyla laterite Microhyla laterite Microhyla laterite Microhyla laterite Microhyla laterite Microhyla malang Microhyla malang	India: Karnataka, MangaloreIndia: Karnataka, ManipalIndia: Karnataka, ManipalIndia: Karnataka, MangaloreIndia: Karnataka, MangaloreIndia: Kerala, Kannur, MadayiparaIndia: Kerala, Kannur, MadayiparaIndia: Kerala, Kasargod, AnakalluMalaysia: Sarawak, Gunung SerapiMalaysia: Sarawak, Gunung Serapi	BNHS 5965 GL3302 SDBDU 2015.3062 SDBDU 2017.3583 SDBDU 2017.3696 SDBDU 2017.3602 KUHE 53018 KUHE:53034	MH807394 KT600670 KT600671 MH807395 MH807396 MH807397 MH807398 AB598319 AB598320
92 93 94 95 96 97 98 99 100 101	Microhyla kodial Microhyla laterite Microhyla laterite Microhyla laterite Microhyla laterite Microhyla laterite Microhyla malang Microhyla malang Microhyla malang	India: Karnataka, MangaloreIndia: Karnataka, ManipalIndia: Karnataka, ManipalIndia: Karnataka, MangaloreIndia: Karnataka, MangaloreIndia: Kerala, Kannur, MadayiparaIndia: Kerala, Kannur, MadayiparaIndia: Kerala, Kasargod, AnakalluMalaysia: Sarawak, Gunung SerapiMalaysia: Sarawak, Gunung SerapiMalaysia: Sarawak, Gunung SerapiMalaysia: Sarawak, Gunung Serapi	BNHS 5965 GL3302 SDBDU 2015.3062 SDBDU 2017.3583 SDBDU 2017.3696 SDBDU 2017.3602 KUHE 53018 KUHE 53034 KUHE NNL M3	MH807394 KT600670 KT600671 MH807395 MH807396 MH807397 MH807398 AB598319 AB598320 AB598321
92 93 94 95 96 97 98 99 100 101 102	Microhyla kodial Microhyla laterite Microhyla laterite Microhyla laterite Microhyla laterite Microhyla laterite Microhyla laterite Microhyla malang Microhyla malang Microhyla malang Microhyla malang	India: Karnataka, MangaloreIndia: Karnataka, ManipalIndia: Karnataka, ManipalIndia: Karnataka, ManipalIndia: Karnataka, MangaloreIndia: Kerala, Kannur, MadayiparaIndia: Kerala, Kannur, MadayiparaIndia: Kerala, Kasargod, AnakalluMalaysia: Sarawak, Gunung SerapiMalaysia: Sarawak, Gunung SerapiMalaysia: Sarawak, Gunung SerapiMalaysia: Sarawak, Kanowit	BNHS 5965 GL3302 SDBDU 2015.3062 SDBDU 2017.3583 SDBDU 2017.3696 SDBDU 2017.3602 KUHE 53018 KUHE:53034 KUHE NNL M3 KUHE:42597	MH807394 KT600670 KT600671 MH807395 MH807396 MH807397 MH807398 AB598319 AB598320 AB598321 AB598322
92           93           94           95           96           97           98           99           100           101	Microhyla kodial Microhyla laterite Microhyla laterite Microhyla laterite Microhyla laterite Microhyla laterite Microhyla malang Microhyla malang Microhyla malang	India: Karnataka, MangaloreIndia: Karnataka, ManipalIndia: Karnataka, ManipalIndia: Karnataka, MangaloreIndia: Karnataka, MangaloreIndia: Kerala, Kannur, MadayiparaIndia: Kerala, Kannur, MadayiparaIndia: Kerala, Kasargod, AnakalluMalaysia: Sarawak, Gunung SerapiMalaysia: Sarawak, Gunung SerapiMalaysia: Sarawak, Gunung SerapiMalaysia: Sarawak, Gunung Serapi	BNHS 5965 GL3302 SDBDU 2015.3062 SDBDU 2017.3583 SDBDU 2017.3696 SDBDU 2017.3602 KUHE 53018 KUHE 53034 KUHE NNL M3	MH807394 KT600670 KT600671 MH807395 MH807396 MH807397 MH807398 AB598319 AB598320 AB598321

106	Microhyla malang	Malaysia: Sabah, Tawau Hills	KUHE NNL M8	AB598326
107	Microhyla malang	Malaysia: Sarawak, Kubah National Park	ZMH A10027	GU154879
108	Microhyla malang	Malaysia: Sarawak, Kubah National Park	ZRC 1.11939	GU154887
109	Microhyla malang	NA	Isolate: KNP1121	KT851978
110	Microhyla malang	NA	Isolate: KNP1055	KT851980
111	Microhyla malang	Indonesia: Kalimantan, Balikpapan	MZB Amp 16364	AB634677
112	Microhyla "sp. 1"	Malaysia: Sabah, Crocker	BOR:8480	AB634678
113	Microhyla mantheyi	Malaysia: Selangor, Templer Park	KUHE 15726	AB598333
114	Microhyla mantheyi	Malaysia: Pahang, Temerloh	KUHE:52556	AB598334
115	Microhyla mantheyi	Malaysia: Selangor, Gombak	KUHE:15726	KM509163
116	Microhyla marmorata	Laos: Houapan, Xamneua	KUHE:32455	AB634668
17	Microhyla mihintalei	Sri Lanka: Anuradhapura	DZ1468	KU214861
118	Microhyla mihintalei	Sri Lanka: Dambulla	DZ1400	KU214856
110	Microhyla mihintalei	Sri Lanka: Makandura	DZ1127	KU214850 KU214857
	~	Sri Lanka: Makandura	DZ1410 DZ1418	
120	Microhyla mihintalei		-	KU214859
121	Microhyla mihintalei	Sri Lanka: Mihinthale	DZ1445	KU214858
22	Microhyla mihintalei	Sri Lanka: Mihinthale	DZ1446	KU214860
23	Microhyla mixtura	China: Sichuan	CIB 20070248	AB634669
24	Microhyla mukhlesuri	Bangladesh: Chittagong, Raozan	IABHU 3879	AB543608
25	Microhyla mukhlesuri	Bangladesh: Chittagong, Raozan	IABHU 3880	AB543609
26	Microhyla mukhlesuri	India: Mizoram	SDBDU 2010.1332	MH549575
27	Microhyla mukhlesuri	Laos: Luang Prabang, Ban Nong Di	K3361	KR827917
128	Microhyla mukhlesuri	Laos: Luang Prabang, Ban Sop Khao	K3090	KR827918
129	Microhyla mukhlesuri	Laos: Luang Prabang, Ban Sop Khao	K3087	KR827919
130	Microhyla mukhlesuri	Laos: Luang Prabang, Ban Nong Di	K3334/2006.2360	KR827920
131	Microhyla mukhlesuri	Laos: Luang Prabang, Ban Sop Khao	K3179/2006.2362	KR827921
32	Microhyla mukhlesuri	Laos: Luang Prabang, Ban Sop Choun	K3216/2006.2381	KR827922
33	Microhyla mukhlesuri	Laos: Luang Prabang, Luang Prabang	K4/1997.8359	KR827925
134	Microhyla mukhlesuri	Laos: Luang Prabang, Ban Vang Thong	K3252/2006.2391	KR827926
135	Microhyla mukhlesuri	Laos: Luang Prabang, Ban Sop Khao	K3154/006.2331	KR827931
136	Microhyla mukhlesuri	Laos: Phongsaly, Long Nai Khao	K1946/2005.0177	KR827928
137	Microhyla mukhlesuri	Laos: Phongsaly, Nathen	K1634/2004.0426	KR827929
138	Microhyla mukhlesuri	Laos: Viangchan, Vientiane	717D	KR827927
139	Microhyla mukhlesuri	Malaysia: Perlis, 9 km W Padang Besar, FRIM field station	JAM 1991	KC822490
140	Microhyla mukhlesuri	Myanmar: Shan, Taunggyi, Ma Gawe Reserve, Kalaw	CAS HERP 230957	KC179995
141	Microhyla mukhlesuri	Thailand: Bangkok, Kasetsart University	0976Y	KR827923
42	Microhyla mukhlesuri	Thailand: Bangkok	KUHE 22064	AB634666
43	Microhyla mukhlesuri	Thailand: Chiang Mai, Doi Chiang Dao	K3009	KR827924
44	Microhyla mukhlesuri	Thailand: Kanchanaburi, Thong Pha Phum	KUHE 35165	AB201186
145	Microhyla mukhlesuri	Thailand: Phang Nga, Phang-nga Breeding Station	P306	KR827930
146	Microhyla mukhlesuri	Vietnam: Quang Binh, Phong Nha-Ke Bang National Park	ZFMK86426	EU157074
147	Microhyla mukhlesuri	Vietnam: Quang Binh, Phong Nha-Ke Bang National Park	ZFMK86370	EU157075
148	Microhyla mukhlesuri	Vietnam: Quang Binh, Phong Nha-Ke Bang National Park	ZFMK86752	EU157076
149	Microhyla mukhlesuri	NA	KIZHERP0138	JX678905
50	Microhyla mukhlesuri	NA	NA	JQ621935
51	Microhyla mukhlesuri	NA	NA	AF215371
52	Microhyla mukhlesuri	NA	NA	AF215373
53	Microhyla mukhlesuri	NA	TZ52	AF285202
155	Microhyla mymensinghensis	Bangladesh: Mymensingh	IABHU F5012 1-6	AB530529
	Microhyla mymensinghensis Microhyla mymensinghensis	Bangladesh: Mymensingh	BdMsp 75-76	AB530529 AB530530
	macronyia mymenstrigriensis	Dangiaucsii. Wryniensingii		
155 156	Microhyla mymensinghensis	Bangladesh: Mymensingh	BdMsp 81	AB530531

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158	Microhyla mymensinghensis	Bangladesh: Mymensingh	BdMsp 72-73	AB530533
159	Microhyla mymensinghensis	Bangladesh: Mymensingh	BdMsp 77-78	AB530534
160	Microhyla mymensinghensis	Bangladesh: Mymensingh	-	AB530535
161	Microhyla mymensinghensis	Bangladesh: Mymensingh	DFBGBAU Msp 306	AB530536
162	Microhyla mymensinghensis	Bangladesh: Sylhet	IABHU 3898	AB543606
163	Microhyla mymensinghensis	Bangladesh: Sylhet	IABHU 3899	AB543607
164	Microhyla mymensinghensis	India: Assam, Maruacherra	ADWII_BM1	MH549577
165	Microhyla mymensinghensis	India: Assam, Maruacherra	ADWII_BM2	MH549578
166	Microhyla mymensinghensis	India: Assam, Silchar	SDBDU 2008.1321	MH549576
167	Microhyla mymensinghensis	India: Manipur, Tamenglong	SDBDU 2007.14	MH549579
168	Microhyla mymensinghensis	India: Manipur, Tamenglong	SDBDU 2008.1440	MH549580
169	Microhyla mymensinghensis	India: Meghalaya, West Garo Hills	SDBDU 2008.1360	MH549581
170	Microhyla mymensinghensis	India: Nagaland, Kohima, Zubza	SDBDU 2007.30	MH549582
171	Microhyla mymensinghensis	India: Nagaland, Kohima, Toulizie	SDBDU 2007.209	MH549583
172	Microhyla mymensinghensis	India: Nagaland, Kohima, Tseminyu	SDBDU 2007.248	MH549584
173	Microhyla mymensinghensis	India: Nagaland, Peren, Intanki NP	SDBDU 2009.37	MH549585
174	Microhyla mymensinghensis	India: Tripura, Gumti WLS	SDBDU 2009.568	MH549586
175	Microhyla mymensinghensis	India: Tripura, Jampui Hills	SDBDU 2009.611	MH549587
176	Microhyla mymensinghensis	India: Tripura, Trishna WLS	SDBDU 2009.482	MH549588
177	Microhyla mymensinghensis	India: Tripura, Sepahijala WLS	SDBDU 2009.444	MH549589
178	Microhyla mymensinghensis	India: West Bengal, Kolkata	SDBDU 2015.2904	MH549590
179	Microhyla nanapollexa	Vietnam: Quang Nam	PT-484	KM509164
180	Microhyla nilphamariensis	Bangladesh: Dinajpur	DB-Hi-FROG 12005	AB201187
181	Microhyla nilphamariensis	Bangladesh: Dinajpur	IABHU 22135	AB530537
182	Microhyla nilphamariensis	Bangladesh: Dinajpur	IABHU 22136	AB530538
183	Microhyla nilphamariensis	Bangladesh: Dinajpur	IABHU 22137	AB530539
184	Microhyla nilphamariensis	Bangladesh: Saidpur	MZH-2360	KP072787
185	Microhyla nilphamariensis	Bangladesh: Saidpur	MZH-2361	KP072788
186	Microhyla nilphamariensis	Bangladesh: Saidpur	MZH-2362	KP072789
187	Microhyla nilphamariensis	Bangladesh: Saidpur	MZH-2363	KP072790
188	Microhyla nilphamariensis	Bangladesh: Saidpur	MZH-2364	KP072791
189	Microhyla nilphamariensis	Bangladesh: Saidpur	MZH-2365	KP072792
190	Microhyla nilphamariensis	Bangladesh: Saidpur	MZH-2366	KP072793
191	Microhyla nilphamariensis	India: Andhra Pradesh, Srikakulam	SDBDU 2007.4987	MH549591
192	Microhyla nilphamariensis	India: Assam, Barpet, Mandia	SDBDU 2015.2905	MH549592
193	Microhyla nilphamariensis	India: Assam, Tezpur, Mazgaon	SDBDU 2015.2915	MH549593
194	Microhyla nilphamariensis	India: Bihar, Banka, Kaitha	SDBDU 2011.869	MH549594
195	Microhyla nilphamariensis	India: Chhattisgarh, Durga Dhara	SDBDU 2010.401	MH549595
196	Microhyla nilphamariensis	India: Delhi, Bawana	SDBDU 2016.3375A	MH549596
197	Microhyla nilphamariensis	India: Karnataka, Bajipe	NA	AB530627
198	Microhyla nilphamariensis	India: Karnataka, Karnoor	BNHS 5028	AB530628
199	Microhyla nilphamariensis	India: Karnataka, Karnoor	BNHS 5029	AB530629
200	Microhyla nilphamariensis	India: Karnataka, Talagini	RBRL 040723-04	AB530630
201	Microhyla nilphamariensis	India: Karnataka, Castle Rock	SDBDU 2011.836	MH549597
202	Microhyla nilphamariensis	India: Karnataka, Kathlekan	SDBDU 2011.1376	MH549598
203	Microhyla nilphamariensis	India: Karnataka, Mangaluru	SDBDU 2015.3045	MH549599
204	Microhyla nilphamariensis	India: Karnataka, Manipal	SDBDU 2015.3060	MH549600
205	Microhyla nilphamariensis	India: Karnataka, Shimoga, Jog	SDBDU 2003.1353	MH549602
206	Microhyla nilphamariensis	India: Kerala, Anakallu	SDBDU 2017.3600	MH549601
207	Microhyla nilphamariensis	India: Kerala, Kakkayam	SDBDU 2008.403	MH549603
208	Microhyla nilphamariensis	India: Kerala, Mannuthy	SDBDU 2003.1345	MH549604
209	Microhyla nilphamariensis	India: Kerala, Kannur, Madayipara	SDBDU 2017.3581	MH549605
210	Microhyla nilphamariensis	India: Maharashtra, Koyna	SDBDU 2004.4507	MH549606
211	Microhyla nilphamariensis	India: Maharashtra, Phansad WLS	SDBDU 2011.1459	MH549607
212	Microhyla nilphamariensis	India: Maharashtra, Amboli	SDBDU 2014.2482	MH549608
213	Microhyla nilphamariensis	India: Maharashtra, Pune	SDBDU 2014.2676	MH549609
214	Microhyla nilphamariensis	India: Maharashtra, Neral	SDBDU 2014.2750	MH549610
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215	Microhyla nilphamariensis	India: Maharashtra, Amboli	SDBDU 2002.1336	MH549611
216	Microhyla nilphamariensis	India: Maharashtra, Amboli	SDBDU 2004.1433	MH549612
217	Microhyla nilphamariensis	India: Maharashtra, Koyna	SDBDU 2007.1562	MH549613
218	Microhyla nilphamariensis	India: Odisha, Balugaon	SDBDU 2015.3121	MH549614
219	Microhyla nilphamariensis	India: Uttarakhand, Dehradun	ADWII_DW1	MH549615
220	Microhyla nilphamariensis	India: Uttarakhand, Tuntowala	ADWII_DT1	MH549616
221	Microhyla nilphamariensis	India: Uttarakhand, Maneri	ADWII_059	MH549617
222	Microhyla nilphamariensis	India: Uttar Pradesh, Rajghat	ADWII_M03	MH549618
223	Microhyla nilphamariensis	Nepal: Mechi, Jhapa, Budhabare	JRK201528	KY655950
224	Microhyla nilphamariensis	Nepal: Mechi, Taplujung, Hangdewa	JRK201529	KY655951
225	Microhyla nilphamariensis	Nepal: Narayani, Chitwan, Jhuwani	JRK201501	KY655926
226	Microhyla nilphamariensis	Nepal: Narayani, Chitwan, Jhuwani	JRK201502	KY655927
227	Microhyla nilphamariensis	Nepal: Narayani, Chitwan, Jhuwani	JRK201503	KY655928
228	Microhyla nilphamariensis	Nepal: Narayani, Chitwan, Jhuwani	JRK201504	KY655929
229	Microhyla nilphamariensis	Nepal: Narayani, Chitwan, Jhuwani	JRK201505	KY655930
230	Microhyla nilphamariensis	Nepal: Narayani, Chitwan, Jhuwani	JRK201506	KY655931
231	Microhyla nilphamariensis	Nepal: Narayani, Chitwan, Jhuwani	JRK201507	KY655932
232	Microhyla nilphamariensis	Nepal: Narayani, Chitwan, Jhuwani	JRK201508	KY655933
233	Microhyla nilphamariensis	Nepal: Narayani, Chitwan, Jhuwani	JRK201509	KY655934
234	Microhyla nilphamariensis	Nepal: Narayani, Chitwan, Jhuwani	JRK201510	KY655935
235	Microhyla nilphamariensis	Nepal: Narayani, Chitwan, Jhuwani	JRK201511	KY655936
236	Microhyla nilphamariensis	Nepal: Narayani, Chitwan, Jhuwani	JRK201512	KY655937
237	Microhyla nilphamariensis	Nepal: Narayani, Chitwan, Jhuwani	JRK201513	KY655938
238	Microhyla nilphamariensis	Nepal: Narayani, Chitwan, Jhuwani	JRK201514	KY655939
239	Microhyla nilphamariensis	Nepal: Narayani, Chitwan, Jhuwani	JRK201515	KY655940
240	Microhyla nilphamariensis	Nepal: Narayani, Chitwan, Jhuwani	JRK201516	KY655941
241	Microhyla nilphamariensis	Nepal: Narayani, Chitwan, Jhuwani	JRK201517	KY655942
242	Microhyla nilphamariensis	Nepal: Narayani, Chitwan, Jhuwani	JRK201518	KY655943
243	Microhyla nilphamariensis	Nepal: Narayani, Chitwan, Jhuwani	JRK201519	KY655944
244	Microhyla nilphamariensis	Nepal: Narayani, Chitwan, Jhuwani	JRK201520	KY655945
245	Microhyla nilphamariensis	Nepal: Narayani, Chitwan, Jhuwani	JRK201521	KY655946
246	Microhyla nilphamariensis	Nepal: Narayani, Chitwan, Jhuwani	JRK201522	KY655947
247	Microhyla nilphamariensis	Nepal: Narayani, Chitwan, Jhuwani	JRK201523	KY655948
248	Microhyla nilphamariensis	Nepal: Narayani, Chitwan, Jhuwani	JRK201524	KY655949
249	Microhyla nilphamariensis	Nepal: Mechi, Taplujung, Hangdewa	JRK201529	KY655951
250	Microhyla okinavensis	Japan: Okinawa	IABHU5263	AB303950
250	Microhyla okinavensis	Japan: Ishigaki	Haplotype: Moki-Jp2	AB530635
252	Microhyla okinavensis	Japan: Ishigaki Island, Okinawa	IABHU5263	NC 010233
252	Microhyla 'okinavensis'	Japan: Ryukyu, Amami, Amamioshima	KUHE12840	AB201184
253	Microhyla 'okinavensis'	Japan: Okinawa	Haplotype: Moki-Jp1	
255	Microhyla orientalis	Indonesia: Bali, Wongaya Gede	KUHE 55073	AB530634 AB781469
255	Microhyla orientalis	Indonesia: Bali, Wongaya Gede	KUHE:55048	AB781409 AB781465
250	Microhyla orientalis	Indonesia: Bali, Wongaya Gede		
			KUHE:55049	AB781466
258	Microhyla orientalis	Indonesia: Bali, Wongaya Gede	KUHE:55050	AB781467
259	Microhyla orientalis	Indonesia: Bali, Wongaya Gede	KUHE:55072	AB781468
260	Microhyla orientalis	Indonesia: Bali, Wongaya Gede	KUHE:55074	AB781470
261	Microhyla orientalis	Indonesia: Bali, Wongaya Gede	KUHE:55076	AB781471
262	Microhyla orientalis	Indonesia: Bali, Wongaya Gede	KUHE:UL M11	AB781472
263	Microhyla orientalis	Indonesia: Bali, Batu Karu	MZB Amp 16259	AB634679
264	Microhyla ornata	India: Andhra Pradesh, Maredumilli	SDBDU 2015.2898	MH549619
265	Microhyla ornata	India: Andhra Pradesh, Maredumilli	SDBDU 2015.2899	MH549620
266	Microhyla ornata	India: Karnataka, Dharwad	ZSIK-A9119	AB201188
267	Microhyla ornata	India: Karnataka, Mudigere	BNHS 5036	AB530632
268	Microhyla ornata	India: Karnataka, Gundlupet	SDBDU 2007.6029	MH549621
269	Microhyla ornata	India: Karnataka, Shimoga	SDBDU 2003.1352	MH549622
270	Microhyla ornata	India: Karnataka, Dandeli	SDBDU 2011.1314	MH549623
271	Microhyla ornata	India: Karnataka, Mysore	SDBDU 2012.1960	MH549624

	10 11			
272	Microhyla ornata	India: Karnataka, Sakleshpur	SDBDU 2012.2198	MH549625
273	Microhyla ornata	India: Karnataka, BR Hills	SDBDU 2014.2539	MH549626
274	Microhyla ornata	India: Karnataka, Bannerghatta	SDBDU 2014.2555	MH549627
275	Microhyla ornata	India: Kerala, Wayanad, Pulpally	RGCB15059	KP072794
276	Microhyla ornata	India: Kerala, Karamana	SDBDU 2015.2970	MH549628
277	Microhyla ornata	India: Kerala, Palakkad	SDBDU 2003.1344	MH549629
278	Microhyla ornata	India: Tamil Nadu, Kiriparai	SDBDU 2008.1958	MH549630
279	Microhyla ornata	India: Tamil Nadu, Kunnapattu	SDBDU 2014.2733A	MH549631
280	Microhyla ornata	India: Tamil Nadu, Mamallapuram	SDBDU 2014.2733B	MH549632
281	Microhyla ornata	India: Tamil Nadu, Coimbatore	SDBDU 2014.2794	MH549633
282	Microhyla ornata	India: Tamil Nadu, Siruvani	SDBDU 2014.2820	MH549634
283	Microhyla ornata	India: Tamil Nadu, Coimbatore	SDBDU 2003.1341	MH549635
284	Microhyla ornata	India: Tamil Nadu, Coimbatore	SDBDU 2008.1720	MH549636
285	Microhyla ornata	Sri Lanka: Kumbalagama	DZ 1085	MH807399
286	Microhyla ornata	Sri Lanka: Puttalam	DZ 1104	MH807400
287	Microhyla ornata	Sri Lanka: Makandura	DZ 1426	MH807401
288	Microhyla ornata	Sri Lanka: Makandura	DZ 1427	MH807402
289	Microhyla ornata	Sri Lanka: Kukulamalpotha	DZ 1427	MH807402
289	Microhyla ornata	Sri Lanka: Kukulamalpotha	DZ 1431 DZ 1432	MH807403
290	Microhyla ornata	Sri Lanka: Ampara	DZ 1452 DZ 1460	MH807404 MH807405
291	Microhyla ornata	Sri Lanka: Anuradhapura	DZ 1400	MH807405 MH807406
292	Microhyla ornata	Sri Lanka: Anuradhapura	DZ 1471 DZ 1472	MH807400 MH807407
293 294	Microhyla ornata Microhyla palmipes	Indonesia: Bali	MZB Amp 16255	AB634670
295	Microhyla perparva	Malaysia: Sarawak	KUHE 53675	AB634673
296	Microhyla petrigena	Malaysia: Sarawak	KUHE 53743	AB634675
297	Microhyla pulchra	China: Guangdong	NA	KF798195
298	Microhyla pulchra	Thailand: Kanchanaburi, Thong Pha Phum	KUHE35119	AB201191
299	Microhyla pulchra	Thailand: Kanchaburi, Pilok	KUHE:22113	AB634676
300	Microhyla pulchra	Pet trade	Rds 05	DQ283422
301	Microhyla pulchra	NA	NA	AF215374
302	Microhyla pulchra	NA	TZ299	AF285203
303	Microhyla pulchra	NA	TZ98104	AF285204
304	Microhyla pulchra	NA	TZ98106	AF285205
305	Microhyla pulchra	China: Guangdong, Dongguan, Yingping Moun- tain	NA	NC024547
	<i>, , , ,</i>		16S19	
306	Microhyla pulchra	China: Hainan Province	10319	KU840571
306 307	Microhyla pulchra	China: Hainan Province Vietnam: Lang Son, Huu Lien	K760	KU840571 KR827945
	Microhyla pulchra Microhyla pulchra			
307	Microhyla pulchra Microhyla pulchra	Vietnam: Lang Son, Huu Lien	K760	KR827945
307 308	Microhyla pulchra Microhyla pulchra Microhyla pulchra	Vietnam: Lang Son, Huu Lien Laos: Luang Prabang, Ban Nong Di	K760 2006.2392	KR827945 KR827946
307 308 309	Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra	Vietnam: Lang Son, Huu LienLaos: Luang Prabang, Ban Nong DiLaos: Luang Prabang, Ban Sop Choun	K760 2006.2392 2006.2395	KR827945 KR827946 KR827947
307 308 309 310	Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra	Vietnam: Lang Son, Huu LienLaos: Luang Prabang, Ban Nong DiLaos: Luang Prabang, Ban Sop ChounLaos: Luang Prabang, Luang Prabang	K760 2006.2392 2006.2395 1999.6057	KR827945 KR827946 KR827947 KR827948
307 308 309 310 311	Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra	Vietnam: Lang Son, Huu LienLaos: Luang Prabang, Ban Nong DiLaos: Luang Prabang, Ban Sop ChounLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Luang Prabang	K760 2006.2392 2006.2395 1999.6057 1997.8380	KR827945 KR827946 KR827947 KR827948 KR827949
307 308 309 310 311 312	Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra	Vietnam: Lang Son, Huu LienLaos: Luang Prabang, Ban Nong DiLaos: Luang Prabang, Ban Sop ChounLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Ban Sop Choun	K760 2006.2392 2006.2395 1999.6057 1997.8380 K3100	KR827945 KR827946 KR827947 KR827948 KR827949 KR827950
307 308 309 310 311 312 313	Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra	Vietnam: Lang Son, Huu LienLaos: Luang Prabang, Ban Nong DiLaos: Luang Prabang, Ban Sop ChounLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Ban Sop ChounIndia: Karnataka	K760 2006.2392 2006.2395 1999.6057 1997.8380 K3100 NA	KR827945 KR827946 KR827947 KR827948 KR827949 KR827950 AB201192
307 308 309 310 311 312 313 314	Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla rubra Microhyla rubra Microhyla rubra	Vietnam: Lang Son, Huu LienLaos: Luang Prabang, Ban Nong DiLaos: Luang Prabang, Ban Sop ChounLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Ban Sop ChounIndia: KarnatakaIndia: Karnataka, Shivanahalli	K760 2006.2392 2006.2395 1999.6057 1997.8380 K3100 NA SDBDU 2014.2558A	KR827945 KR827946 KR827947 KR827948 KR827949 KR827950 AB201192 KU214855
307 308 309 310 311 312 313 314 315	Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla rubra Microhyla rubra Microhyla rubra Microhyla rubra	Vietnam: Lang Son, Huu LienLaos: Luang Prabang, Ban Nong DiLaos: Luang Prabang, Ban Sop ChounLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Ban Sop ChounIndia: KarnatakaIndia: Karnataka, ShivanahalliIndia: Karnataka, Bannerghatta	K760 2006.2392 2006.2395 1999.6057 1997.8380 K3100 NA SDBDU 2014.2558A SDBDU 2014.2558B	KR827945 KR827946 KR827947 KR827948 KR827949 KR827950 AB201192 KU214855 MH807408
307 308 309 310 311 312 313 314 315 316	Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla rubra Microhyla rubra Microhyla rubra	Vietnam: Lang Son, Huu LienLaos: Luang Prabang, Ban Nong DiLaos: Luang Prabang, Ban Sop ChounLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Ban Sop ChounIndia: KarnatakaIndia: Karnataka, ShivanahalliIndia: Karnataka, BannerghattaIndia: Karnataka, BR Hills	K760 2006.2392 2006.2395 1999.6057 1997.8380 K3100 NA SDBDU 2014.2558A SDBDU 2014.2558B SDBDU 2014.2548	KR827945 KR827946 KR827947 KR827948 KR827949 KR827950 AB201192 KU214855 MH807408 MH807409
307           308           309           310           311           312           313           314           315           316           317           318	Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla rubra Microhyla rubra Microhyla rubra Microhyla rubra Microhyla rubra Microhyla rubra Microhyla rubra	Vietnam: Lang Son, Huu LienLaos: Luang Prabang, Ban Nong DiLaos: Luang Prabang, Ban Sop ChounLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Ban Sop ChounIndia: KarnatakaIndia: Karnataka, ShivanahalliIndia: Karnataka, BannerghattaIndia: Karnataka, ShimogaIndia: Kerala, Mannuthy	K760 2006.2392 2006.2395 1999.6057 1997.8380 K3100 NA SDBDU 2014.2558A SDBDU 2014.2558B SDBDU 2014.2548 SDBDU 2003.1356 SDBDU 2003.1337	KR827945           KR827946           KR827947           KR827948           KR827949           KR827950           AB201192           KU214855           MH807408           MH807410           MH807411
307 308 309 310 311 312 313 314 315 316 317 318 319	Microhyla pulchraMicrohyla pulchraMicrohyla pulchraMicrohyla pulchraMicrohyla pulchraMicrohyla pulchraMicrohyla pulchraMicrohyla rubraMicrohyla rubra	Vietnam: Lang Son, Huu LienLaos: Luang Prabang, Ban Nong DiLaos: Luang Prabang, Ban Sop ChounLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Ban Sop ChounIndia: KarnatakaIndia: Karnataka, ShivanahalliIndia: Karnataka, BannerghattaIndia: Karnataka, BR HillsIndia: Karnataka, ShimogaIndia: Kerala, MannuthyIndia: Kerala, Parambikulam	K760 2006.2392 2006.2395 1999.6057 1997.8380 K3100 NA SDBDU 2014.2558A SDBDU 2014.2558B SDBDU 2014.2548 SDBDU 2003.1356 SDBDU 2003.1337 SDBDU 2003.1340	KR827945           KR827946           KR827947           KR827948           KR827949           KR827950           AB201192           KU214855           MH807408           MH807410           MH807411           MH807412
307 308 309 310 311 312 313 314 315 316 317 318 319 320	Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla rubra Microhyla rubra Microhyla rubra Microhyla rubra Microhyla rubra Microhyla rubra Microhyla rubra Microhyla rubra	Vietnam: Lang Son, Huu LienLaos: Luang Prabang, Ban Nong DiLaos: Luang Prabang, Ban Sop ChounLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Ban Sop ChounIndia: KarnatakaIndia: Karnataka, ShivanahalliIndia: Karnataka, BannerghattaIndia: Karnataka, BR HillsIndia: Kerala, MannuthyIndia: Kerala, ParambikulamIndia: Tamil Nadu, Mamallapuram	K760 2006.2392 2006.2395 1999.6057 1997.8380 K3100 NA SDBDU 2014.2558A SDBDU 2014.2558B SDBDU 2014.2548 SDBDU 2014.2548 SDBDU 2003.1356 SDBDU 2003.1340 SDBDU 2014.2753A	KR827945KR827946KR827947KR827948KR827949KR827950AB201192KU214855MH807408MH807409MH807410MH807411MH807412MH807413
307           308           309           310           311           312           313           314           315           316           317           318           319           320           321	Microhyla pulchraMicrohyla pulchraMicrohyla pulchraMicrohyla pulchraMicrohyla pulchraMicrohyla pulchraMicrohyla pulchraMicrohyla rubraMicrohyla rubra	Vietnam: Lang Son, Huu LienLaos: Luang Prabang, Ban Nong DiLaos: Luang Prabang, Ban Sop ChounLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Ban Sop ChounIndia: KarnatakaIndia: Karnataka, ShivanahalliIndia: Karnataka, BannerghattaIndia: Karnataka, BR HillsIndia: Kerala, MannuthyIndia: Kerala, ParambikulamIndia: Tamil Nadu, MamallapuramIndia: Tamil Nadu, Mamallapuram	K760 2006.2392 2006.2395 1999.6057 1997.8380 K3100 NA SDBDU 2014.2558A SDBDU 2014.2558B SDBDU 2014.2548 SDBDU 2014.2548 SDBDU 2003.1356 SDBDU 2003.1340 SDBDU 2014.2753A SDBDU 2014.2753B	KR827945KR827946KR827947KR827948KR827949KR827950AB201192KU214855MH807408MH807409MH807410MH807411MH807412MH807413MH807414
307           308           309           310           311           312           313           314           315           316           317           318           319           320           321           322	Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla rubra Microhyla rubra	Vietnam: Lang Son, Huu LienLaos: Luang Prabang, Ban Nong DiLaos: Luang Prabang, Ban Sop ChounLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Ban Sop ChounIndia: KarnatakaIndia: Karnataka, ShivanahalliIndia: Karnataka, BannerghattaIndia: Karnataka, BR HillsIndia: Kerala, MannuthyIndia: Kerala, ParambikulamIndia: Tamil Nadu, MamallapuramIndia: Tamil Nadu, Coimbatore	K760 2006.2392 2006.2395 1999.6057 1997.8380 K3100 NA SDBDU 2014.2558A SDBDU 2014.2558B SDBDU 2014.2558B SDBDU 2014.2558B SDBDU 2003.1356 SDBDU 2003.1337 SDBDU 2003.1340 SDBDU 2014.2753A SDBDU 2014.2753B SDBDU 2014.2784	KR827945KR827946KR827947KR827948KR827949KR827950AB201192KU214855MH807408MH807409MH807410MH807411MH807412MH807413MH807414MH807415
307           308           309           310           311           312           313           314           315           316           317           318           319           320           321           322           323	Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla rubra Microhyla rubra	Vietnam: Lang Son, Huu LienLaos: Luang Prabang, Ban Nong DiLaos: Luang Prabang, Ban Sop ChounLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Ban Sop ChounIndia: KarnatakaIndia: Karnataka, ShivanahalliIndia: Karnataka, BannerghattaIndia: Karnataka, BR HillsIndia: Kerala, MannuthyIndia: Kerala, ParambikulamIndia: Tamil Nadu, MamallapuramIndia: Tamil Nadu, CoimbatoreIndia: Tamil Nadu, Coimbatore	K760 2006.2392 2006.2395 1999.6057 1997.8380 K3100 NA SDBDU 2014.2558A SDBDU 2014.2558B SDBDU 2014.2558B SDBDU 2014.2548 SDBDU 2003.1356 SDBDU 2003.1337 SDBDU 2003.1340 SDBDU 2014.2753A SDBDU 2014.2753B SDBDU 2014.2784 SDBDU 2014.2789	KR827945KR827946KR827946KR827947KR827948KR827949KR827950AB201192KU214855MH807408MH807409MH807410MH807411MH807412MH807413MH807414MH807415MH807416
307           308           309           310           311           312           313           314           315           316           317           318           319           320           321           322           323           324	Microhyla pulchraMicrohyla pulchraMicrohyla pulchraMicrohyla pulchraMicrohyla pulchraMicrohyla pulchraMicrohyla pulchraMicrohyla pulchraMicrohyla rubraMicrohyla rubra	Vietnam: Lang Son, Huu LienLaos: Luang Prabang, Ban Nong DiLaos: Luang Prabang, Ban Sop ChounLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Ban Sop ChounIndia: KarnatakaIndia: Karnataka, ShivanahalliIndia: Karnataka, BannerghattaIndia: Karnataka, BR HillsIndia: Kerala, MannuthyIndia: Kerala, ParambikulamIndia: Tamil Nadu, MamallapuramIndia: Tamil Nadu, CoimbatoreIndia: Tamil Nadu, CoimbatoreIndia: Tamil Nadu, Coimbatore	K760 2006.2392 2006.2395 1999.6057 1997.8380 K3100 NA SDBDU 2014.2558A SDBDU 2014.2558B SDBDU 2014.2558B SDBDU 2014.2548 SDBDU 2003.1356 SDBDU 2003.1337 SDBDU 2003.1340 SDBDU 2014.2753A SDBDU 2014.2753B SDBDU 2014.2784 SDBDU 2014.2789 SDBDU 2014.2808	KR827945           KR827946           KR827947           KR827948           KR827949           KR827950           AB201192           KU214855           MH807408           MH807410           MH807411           MH807412           MH807413           MH807414           MH807415           MH807416           MH807417
307           308           309           310           311           312           313           314           315           316           317           318           319           320           321           322           323	Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla pulchra Microhyla rubra Microhyla rubra	Vietnam: Lang Son, Huu LienLaos: Luang Prabang, Ban Nong DiLaos: Luang Prabang, Ban Sop ChounLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Luang PrabangLaos: Luang Prabang, Ban Sop ChounIndia: KarnatakaIndia: Karnataka, ShivanahalliIndia: Karnataka, BannerghattaIndia: Karnataka, BR HillsIndia: Kerala, MannuthyIndia: Kerala, ParambikulamIndia: Tamil Nadu, MamallapuramIndia: Tamil Nadu, CoimbatoreIndia: Tamil Nadu, Coimbatore	K760 2006.2392 2006.2395 1999.6057 1997.8380 K3100 NA SDBDU 2014.2558A SDBDU 2014.2558B SDBDU 2014.2558B SDBDU 2014.2548 SDBDU 2003.1356 SDBDU 2003.1337 SDBDU 2003.1340 SDBDU 2014.2753A SDBDU 2014.2753B SDBDU 2014.2784 SDBDU 2014.2789	KR827945KR827946KR827946KR827947KR827948KR827949KR827950AB201192KU214855MH807408MH807409MH807410MH807411MH807412MH807413MH807414MH807415MH807416

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328	Microhyla sholigari	India	VUB 0066	AF249060
329	Microhyla sholigari	India: Talapu, Madikeri	RBRL 060709-29	AB530631
330	Microhyla sholigari	India	VUB 0066	AY948728
331	Microhyla sholigari	India: Karnataka, Bisle	GL3352	KT600672
332	Microhyla sholigari	India: Karnataka, Bisle	GL3353	KT600673
333	Microhyla sholigari	India: Karnataka, BRTTR	GL3360	KT600674
334	Microhyla sholigari	India: Karnataka, BRTTR	GL3361	KT600675
335	Microhyla sholigari	India: Karnataka, BRTTR	GL3362	KT600676
336	Microhyla sholigari	India: Karnataka, Bhagamandala	SDBDU 2011.208	MH807421
337	Microhyla sholigari	India: Karnataka, BR Hills	SDBDU 2014.2528	MH807422
338	Microhyla sholigari	India: Karnataka, BR Hills	SDBDU 2014.2529	MH807423
339	Microhyla sholigari	India: Karnataka, BR Hills	SDBDU 2014.2591	MH807424
340	Microhyla sholigari	India: Karnataka, Gundlupet SDBDU 2007.6033		MH807425
341	Microhyla sholigari	India: Karnataka, Shimoga	SDBDU 2011.40	MH807426
342	Microhyla sholigari	India: Tamil Nadu, Masinagudi	SDBDU 2003.66	MH807427
343	Microhyla superciliaris	Malaysia: Negeri Sembilan, Kenaboi	KUHE 53371	AB634683
344	Microhyla taraiensis	Nepal: Mechi, Jhapa, Jamun Khadi	JRK201525	KY655952
345	Microhyla taraiensis	Nepal: Mechi, Jhapa, Jamun Khadi	JRK201526	KY655953
346	Microhyla taraiensis	Nepal: Mechi, Jhapa, Jamun Khadi	JRK201527	KY655954
347	Microhyla zeylanica	Sri Lanka: Horton plains	DZ 1419	MH807428
	Outgroup			
348	Kaloula pulchra	Thailand: Kanchanaburi	KUHE 35171	AB201194

**Table S2.** Inter- and intraspecific uncorrected p-distances (in percent) for the mitochondrial 16S rRNA gene sequences, within and among members comprising the various South Asian *Microhyla* groups recognized in the study.

	Microhyla achatina GRO	UP			
Intraspecific		Mean	Min	Max	St Dev
Microhyla achatina		1.7	0	2.8	1.3
Microhyla borneensis		0.2	0	1.0	0.3
Microhyla kodial		-	_	_	_
Microhyla malang		1.6	0	3.8	1.2
Microhyla mantheyi		0.7	0	1.0	0.6
Microhyla orientalis		0.04	0	0.2	0.08
Microhyla "sp. 1"		_	_	_	_
Microhyla "sp. 3"		2.6	_	_	_
Interspecific		Mean	Min	Max	St Dev
Microhyla achatina	Microhyla borneensis	6.2	5.8	6.8	0.2
Microhyla achatina	Microhyla kodial	7.8	7.4	8.3	0.4
Microhyla achatina	Microhyla malang	7.0	5.8	8.0	0.5
Microhyla achatina	Microhyla mantheyi	5.8	5.4	6.4	0.4
Microhyla achatina	Microhyla orientalis	5.7	5.4	5.8	0.2
Microhyla achatina	Microhyla "sp. 1"	7.5	7.0	7.8	0.4
Microhyla achatina	Microhyla "sp. 3"	5.2	4.6	5.8	0.5
Microhyla borneensis	Microhyla kodial	7.2	6.8	7.8	0.3
Microhyla borneensis	Microhyla malang	2.5	1.7	3.4	0.3
Microhyla borneensis	Microhyla mantheyi	5.3	4.9	5.6	0.2
Microhyla borneensis	Microhyla orientalis	4.2	4.0	4.5	0.1
Microhyla borneensis	Microhyla "sp. 1"	3.0	2.6	3.2	0.1
Microhyla borneensis	Microhyla "sp. 3"	6.2	6.0	6.6	0.2
Microhyla kodial	Microhyla malang	8.4	7.8	10.0	0.6
Microhyla kodial	Microhyla mantheyi	7.3	7.2	7.4	0.1
Microhyla kodial	Microhyla orientalis	7.2	7.2	7.4	0.1
Microhyla kodial	Microhyla "sp. 1"	7.8	_	-	_
Microhyla kodial	Microhyla "sp. 3"	8.4	8.3	8.4	0.1

Microhyla malang	Microhyla mantheyi	6.2	5.8	7.1	0.3
Microhyla malang	Microhyla orientalis	5.0	4.4	6.4	0.5
Microhyla malang	Microhyla "sp. 1"	3.7	3.4	5.4	
Microhyla malang	Microhyla "sp. 3"	6.8	6.2	7.5	0.4
Microhyla mantheyi	Microhyla orientalis	5.1	4.9	5.2	0.1
Microhyla mantheyi	Microhyla "sp. 1"	5.2	5.0	5.4	0.2
Microhyla mantheyi	Microhyla "sp. 3"	5.5	5.2	5.6	0.2
Microhyla orientalis	Microhyla "sp. 1"	5.6	_	_	_
Microhyla orientalis	Microhyla "sp. 3"	6.3	6.0	6.4	0.1
Microhyla "sp. 1"	Microhyla "sp. 3"	6.8	6.6	7.0	0.3
	Microhyla 'heymonsi' CLADE				
Intraspecific		Mean	Min	Max	St De
Microhyla heymonsi clade 1		0.6	0	2.7	0.9
Microhyla heymonsi clade 2		1.4	0.2	2.5	0.8
Microhyla heymonsi clade 3		1.9	0.3	2.8	0.9
Microhyla heymonsi clade 4		1.6	0	2.6	0.8
Microhyla heymonsi clade 5		0.8	0	1.3	0.4
Microhyla heymonsi clade 6		0.3	0	0.5	0.3
Interspecific		Mean	Min	Max	St De
M. heymonsi clade 1	M. heymonsi clade 2	3.2	2.5	4.6	0.6
M. heymonsi clade 1	M. heymonsi clade 3	5.0	4.4	5.7	0.3
M. heymonsi clade 1	M. heymonsi clade 4	5.0	4.2	6.4	0.6
M. heymonsi clade 1	M. heymonsi clade 5	4.7	3.9	5.4	0.4
M. heymonsi clade 1	M. heymonsi clade 6	5.2	4.9	6.0	0.3
<i>M. heymonsi</i> clade 2	M. heymonsi clade 3	3.7	3.0	4.5	0.4
<i>M. heymonsi</i> clade 2	M. heymonsi clade 4	3.8	2.7	5.4	0.9
M. heymonsi clade 2	M. heymonsi clade 5	3.9	3.1	4.6	0.4
<i>M. heymonsi</i> clade 2	M. heymonsi clade 6	4.5	4.0	4.9	0.3
<i>M. heymonsi</i> clade 3	M. heymonsi clade 4	3.6	2.6	4.7	0.5
M. heymonsi clade 3	M. heymonsi clade 1 M. heymonsi clade 5	3.5	2.6	4.0	0.3
M. heymonsi clade 3	M. heymonsi clade 6	3.5	3.3	3.9	0.2
M. heymonsi clade 4	M. heymonsi clade 5	3.0	2.3	4.0	0.5
M. heymonsi clade 4	M. heymonsi clade 6	4.3	3.9	5.2	0.4
M. heymonsi clade 5	M. heymonsi clade 6	2.7	2.5	2.8	0.1
in neymonsi ciade s	Microhyla berdmorei GROUP		2.5	2.0	0.1
Intraspecific		Mean	Min	Max	St De
Microhyla berdmorei		2.0	0	5.2	1.2
Microhyla cf. berdmorei		_	_	_	_
Microhyla pulchra		1.2	0	2.9	0.7
Interspecific		Mean	Min	Max	St De
Microhyla berdmorei	Microhyla cf. berdmorei	8.9	7.9	10.4	0.7
Microhyla berdmorei	Microhyla pulchra	9.0	7.3	12.3	1.2
Microhyla cf. berdmorei	Microhyla pulchra	11.3	10.2	13.0	1.2
	Microhyla fissipes GROU			·	
Intraspecific		Mean	Min	Max	St De
Microhyla chakrapanii		-	_	-	-
Microhyla fissipes		0	_	-	-
Microhyla mukhlesuri		1.5	0	3.3	0.8
Microhyla mymensinghensis		0.7	0	2.1	0.6
Interspecific		Mean	Min	Max	St De
Microhyla chakrapanii	Microhyla fissipes	2.9	2.9	2.9	
Microhyla chakrapanii	Microhyla mukhlesuri	4.9	3.7	6.2	0.9
Microhyla chakrapanii	Microhyla mymensinghensis	2.6	2.3	3.1	0.2
Microhyla fissipes	Microhyla mukhlesuri	2.4	1.4	3.3	0.5
Microhyla fissipes	Microhyla mymensinghensis	3.1	2.7	3.7	0.3
Microhyla mukhlesuri	Microhyla mymensinghensis	4.1	2.8	5.4	0.6
Microhyla fissipes	Microhyla 'fissipes'	1.0	1.0	1.0	_

	Microhyla ornata GROUP				
Intraspecific		Mean	Min	Max	St De
Microhyla ornata		0.2	0	0.8	0.2
Microhyla nilphamariensis		0.6	0	2.3	0.6
Microhyla taraiensis		0.3	0	0.4	0.2
Interspecific		Mean	Min	Max	St De
Microhyla ornata	Microhyla nilphamariensis	4.6	3.8	5.5	0.3
Microhyla ornata	Microhyla taraiensis	6.5	6.1	7.0	0.2
Microhyla nilphamariensis	Microhyla taraiensis	4.6	4.0	5.7	0.3
	Microhyla rubra GROUP	·			
Intraspecific		Mean	Min	Max	St D
Microhyla mihintalei		0.06	0	0.2	0.0
Microhyla rubra		0.1	0	0.6	0.2
Interspecific		Mean	Min	Max	St D
Microhyla mihintalei	Microhyla rubra	2.6	2.5	3.2	0.2
	Microhyla zeylanica GROUF	)			
Intraspecific		Mean	Min	Max	St D
Microhyla darreli sp. nov.		_	_	_	_
Microhyla karunaratnei		0	_	_	_
Microhyla laterite		0.8	0	1.3	0.6
Microhyla sholigari		0.05	0	0.4	0.1
Microhyla zeylanica		_	_	_	_
Interspecific		Mean	Min	Max	St D
Microhyla darreli sp. nov.	Microhyla karunaratnei	2.5	2.5	2.5	-
Microhyla darreli sp. nov.	Microhyla laterite	4.0	3.8	4.2	0.2
Microhyla darreli sp. nov.	Microhyla sholigari	3.1	3.1	3.3	0.1
Microhyla darreli sp. nov.	Microhyla zeylanica	5.0	_	_	-
Microhyla karunaratnei	Microhyla laterite	3.9	3.7	4.0	0.2
Microhyla karunaratnei	Microhyla sholigari	4.5	4.4	4.6	0.0
Microhyla karunaratnei	Microhyla zeylanica	5.2	_	_	-
Microhyla laterite	Microhyla sholigari	4.4	4.2	4.6	0.1
Microhyla laterite	Microhyla zeylanica	4.2	3.8	4.6	0.4
Microhyla sholigari	Microhyla zeylanica	5.4	5.4	5.8	0.2

**Table S3.** Principal component analysis (PCA) factor loadings and percent variance explained by principal components of eigenvalue > 1.0, based on 40 morphometric variables from 100 adult male specimens representing 20 *Microhyla* species. Values in bold indicate variables with the highest loadings.

S.No	Variables	Factor 1	Factor 2	Factor 3	Factor 4
1	SVL	-0.961473	-0.048706	0.121934	0.026525
2	HW	-0.949378	-0.034903	0.139075	0.070171
3	HL	-0.926951	0.050715	0.133557	0.104290
4	SL	-0.926697	0.148882	0.121104	0.015188
5	EL	-0.913601	-0.165394	0.135525	0.070825
6	EN	-0.869086	-0.042752	0.110472	0.053621
7	NS	-0.887881	0.123156	-0.199513	0.124432
8	IUE	-0.843068	-0.179646	0.029925	0.019324
9	UEW	-0.815663	-0.363995	0.259646	0.099218
10	IN	-0.906025	0.067958	-0.101867	-0.029130
11	FAL	-0.927564	-0.038072	0.086476	0.070105
12	HAL	-0.972806	0.000692	0.124442	0.050439
13	$FL_{I}$	-0.748454	0.387926	0.223972	-0.056414
14	FL <sub>II</sub>	-0.852179	0.237125	0.149129	-0.026511
15	FL <sub>III</sub>	-0.941854	0.089046	0.055188	-0.025939
16	FL <sub>IV</sub>	-0.214467	0.194111	0.134444	0.156749

17	FD <sub>I</sub>	-0.891861	0.082376	0.147549	-0.101715
18	FWI	-0.887133	0.026258	0.155814	-0.128346
19	FD <sub>II</sub>	-0.854753	0.250554	-0.040339	-0.068768
20	FWII	-0.821018	-0.030001	0.213026	-0.118507
21	FD <sub>III</sub>	-0.771784	0.453156	-0.245004	-0.118967
22	FWIII	-0.856830	0.108741	0.151748	-0.179046
23	FD <sub>IV</sub>	-0.303431	0.176112	0.016693	0.031051
24	FW <sub>IV</sub>	-0.882019	0.013184	0.184628	-0.078773
25	THL	-0.961490	0.153262	0.087994	0.061465
26	SHL	-0.919725	0.291703	0.081107	0.025067
27	FOL	-0.936678	0.274438	0.073032	0.052389
28	TFOL	-0.927851	0.262493	0.040773	0.032605
29	TDI	-0.888210	-0.070376	-0.290890	0.040551
30	TWI	-0.757765	-0.490246	-0.231781	0.016398
31	TD <sub>II</sub>	-0.713197	0.242175	-0.505009	-0.029240
32	TW <sub>Π</sub>	-0.711918	-0.577227	-0.184737	-0.079746
33	TD <sub>III</sub>	-0.718442	0.373926	-0.500612	0.027594
34	TWIII	-0.684523	-0.576945	-0.237993	-0.023299
35	TD <sub>IV</sub>	-0.704513	0.428949	-0.478196	0.021295
36	TW <sub>IV</sub>	-0.714914	-0.485291	-0.191782	-0.092892
37	TD <sub>v</sub>	0.014400	-0.029844	0.060019	-0.919668
38	TW <sub>v</sub>	-0.698216	-0.417498	-0.295790	-0.097331
39	IMTL	-0.811457	-0.446738	0.100973	0.039013
40	OMTL	-0.590805	-0.738483	0.023192	0.085111
	Eigenvalue	26.70677	3.51760	1.66609	1.07849
0	% Total variance	66.76693	8.79401	4.16523	2.69623
(	Cum Eigenvalue	26.70677	30.22437	31.89047	32.96896
	Cumulative %	66.7669	75.5609	79.7262	82.4224

Table S4. Acoustic properties of the studied Microhyla species. The mean, standard deviation, maximum, and minimum values are calculated for five calls of each species; median values provided for number of pulses per call.

Species	Voucher	Locality	Call Duration	Call Rise time	Call Fall Time	Pulses/	Pulse Rate	Dominant	CRT/
ı			(sm)	(CRT) (ms)	(CFT) (ms)	Call	(pulses/s)	Frequency (kHz)	CFT Ratio
South Asian species									
M. kodial	SDBDU 2017.3673	India: Karnataka, Baikampady	$261.4\pm26.6$	112.2±28.1	$137.8\pm 28.6$	$6\pm0.5$	$18.0\pm0.5$	$3.8\pm0$	0.9:1.0
			(c.002 - 0.022)	(0.021 - 0.10)	(1.401 - 0.201)	(0-c)	(0.01 - C./1)	(0.0-0.0)	
M. mymensinghensis	SDBDU 2015.2905	India: Assam, Mandia	$466.4 \pm 10.1$	$333.4\pm38.5$	$79.8 \pm 13.7$	$21\pm1.1$	$43.1\pm2.9$	$3.6\pm0.4$	4.3:1.0
			(450.2 - 477.1)	(280.1 - 370.4)	(68.8 - 102.6)	(19-22)	(39.0 - 47.2)	(3.5 - 3.6)	
M. nilphamariensis	SDBDU 2014.2482	India: Maharashtra, Amboli	$337.2 \pm 24.2$	$240.6\pm 22.8$	$82.8 \pm 34.2$	$11\pm0.8$	$29.6 \pm 0.4$	$2.3\pm0$	3.5:1.0
			(311.3 - 368.7)	(211.3 - 274.8)	(38.6 - 127.9)	(10-12)	(29.2 - 30.2)	(2.3 - 2.3)	
M. ornata	SDBDU 2014.2794	India: Tamil Nadu, Coimbatore	$333.8 \pm 24.8$	$193.4\pm 27.1$	$129.8 \pm 23.2$	$13\pm0.4$	$37.3 \pm 1.4$	$2.6\pm0$	1.5:1.0
			(321.1 - 378.6)	(152.6 - 215.3)	(112.2 - 164.4)	(13 - 14)	(34.9 - 38.2)	(2.6 - 2.6)	
M. mihintalei	DZ 1445	Sri Lanka: Anuradhapura,	$162.6 \pm 4.9$	$76.8 \pm 8.5$	$79.2\pm16.2$	$12 \pm 0.4$	$68.4 \pm 2.1$	$2.3\pm0.1$	1.0:1.0
		Mihintale	(158.5–171.7)	(66.2 - 84.3)	(60.1 - 105.1)	(11 - 12)	(65.8 - 70.5)	(2.3 - 2.4)	
M. rubra	SDBDU 2014.2791	India: Tamil Nadu, Coimbatore	$130.6.4 \pm 10.4$	$69.8 \pm 20.5$	$60.8\pm15.7$	$11\pm 1$	$80.4 \pm 3.8$	$2.2 \pm 0.7$	1.3:1.0
			(115.3 - 142.4)	(35.1 - 90.3)	(39.1 - 80.3)	(10 - 12)	(73.8 - 83.3)	(2.0 - 2.2)	
M. darreli sp. nov.	SDBDU 2009.101	India: Kerala, Chathankod	$653.8\pm 55.9$	$516.4 \pm 76.8$	$97.2 \pm 27.7$	$68 \pm 5.5$	$105.6 \pm 1.2$	$3.6\pm0$	5.9:1.0
			(590.3 - 736.2)	(468.6 - 651.3)	(63.8 - 131.8)	(63 - 78)	(103.9 - 106.7)	(3.6 - 3.6)	
M. karunaratnei	DZ 1530	Sri Lanka: Rathnapura,	$869.4 \pm 129.2$	$647.4 \pm 144.2$	$141.4 \pm 28.4$	$60\pm13$	$76.1 \pm 4.4$	$3.2 \pm 1.4$	5.0:1.0
		Morningside forest reserve	(766.3 - 1003.1)	(519.3 - 872.9)	(98.1–175.7)	(56 - 86)	(72.2 - 81.5)	(3.1 - 3.4)	
M. laterite	SDBDU 2015.3062	India: Karnataka, Manipal	$809.6 \pm 60.9$	$673.4 \pm 102.7$	$80.4 \pm 21.9$	$104\pm7$	$128.0 \pm 1.2$	$3.6 {\pm} 0.4$	9.1:1.0
			(727.1 - 886.4)	(542.1 - 823.8)	(62.4 - 111.8)	(94 - 113)	(126.3 - 129.5)	(3.5 - 3.6)	
M. sholigari	SDBDU 2014.2537	India: Karnataka, Biligirirangan	$933.4 \pm 45.7$	$728.8 \pm 58.3$	$149.1 \pm 22.8$	$72 \pm 3.7$	$77.3 \pm 0.4$	$3.4\pm0$	5.0:1.0
		Hills	(901.1 - 1012.4)	(662.9 - 843.7)	(115.8 - 177.1)	(70-79)	(76.9 - 77.8)	(3.4 - 3.4)	
M. zeylanica	DZ 1420	Sri Lanka: Horton Plains	$1759.5 \pm 39.4$	$870.5 \pm 212.8$	$773.3 \pm 161.5$	$86 \pm 3.6$	$48.4 \pm 1.0$	2.7±2.9	1.2:1.0
		National Park	(1/05.2 - 1804.3)	(609.4 - 10/4.3)	(602.4 - 9/6.8)	(81 - 90)	(4/.1-49.6)	(2.3 - 5.0)	
Southeast and East Asian species	Asian species								
M. achatina	UIMZ 0031	Indonesia: Java, Bogor	$228.6 \pm 71.4$	$103.2 \pm 36.5$	$109.6\pm50.9$	8±2	$26.4 \pm 1.1$	$3.3\pm0.8$	1.0:1.0
			(c.cd2-2.011)	(58.4 - 122.5)	(40.2 - 105.2)	(4-9)	(C.82 - 0.02)	(5.2 - 5.4)	
Mfissipes	CIB HN034	China: Hainan Island, Chengmai	$236.2\pm 8.5$ (229.2-251.3)	$149.2 \pm 13.1$ (130.2 - 163.3)	$87.6 \pm 12.4$ (69.2 - 104.4)	$15\pm0.5$ (15-16)	$61.8\pm0.4$ (61.4-62.5)	$3.0\pm0.1$ (3.0-3.1)	1.8:1.0
M. orientalis	UIMZ 0037	Indonesia: Bali. Wongaya Gede	$(62\pm 8.0)$	22.6±0.1	39.6±7.7	<u>5</u> ±0.9	57.7±8.5	3.7±0.0	0.6:1.0
		)	(48.2 - 67.4)	(22.1 - 23.2)	(26.2 - 44.1)	(3-5)	(46.5 - 64.5)	(3.7 - 3.7)	
M. palmipes	not preserved	Indonesia: Java, Telaga Warna	109.6±43.8	$33.2\pm9.7$	$67.2\pm27.0$	$11 \pm 3.2$	79.8±7.6	$3.5\pm0.3$	0.5:1.0
			(104.4)	(7.04-1.07)	(1.001-2.00)	$(c_{1}-0)$	(6.06-0.01)	(0.0-4.0)	

of Microhyla species discussed in the text. Measurement abbreviations and museum acronyms are provided in the Material and methods section. HT holotype; PT	eferred specimen. All measurements are in millimeters (mm).
hyla species discussed in the	pecimen. All measurements

									South	South Asian sj	species											
									Mic	Microhyla kodial	dial											
Vocuher No	status	sex	SVL	ΜH	HL	SL	EL	EN	SN	IUE	UEW	Z	FAL	HAL	FIL	FIIL	FIIIL	FIVL	FDI	FWI	FDII	FWII
SDBDU 2017.3675	RS	Μ	18.2	5.9	4.0	2.2	1.8	1.5	0.9	2.0	1.5	1.4	2.9	3.9	0.5	1.2	2.3	1.4	0.3	0.3	0.3	0.3
SDBDU 2017.3689	RS	М	15.0	4.9	3.9	2.0	1.5	1.0	0.7	1.7	1.4	1.2	2.3	3.1	0.4	1.0	2.0	1.4	0.2	0.2	0.3	0.3
SDBDU 2017.3673	RS	Μ	16.2	4.8	3.9	2.0	1.4	1.2	0.7	1.8	1.0	1.3	2.8	3.6	0.3	1.0	2.2	1.4	0.2	0.2	0.4	0.4
SDBDU 2017.3674	RS	Σ	17.2	4.8	3.8	2.1	1.5	1.3	0.7	1.9	1.3	1.3	2.8	3.8	0.4	1.1	2.2	1.4	0.3	0.3	0.4	0.4
SDBDU 2017.3676	RS	Μ	17.8	5.6	4.0	2.1	1.6	1.4	0.8	1.8	1.2	1.3	2.7	3.9	0.3	1.0	2.4	1.3	0.2	0.2	0.3	0.3
SDBDU 2017.3688	RS	Μ	14.2	4.8	3.9	1.9	1.4	1.1	0.7	1.7	1.0	1.1	2.3	3.4	0.4	1.0	2.0	1.2	0.2	0.2	0.2	0.2
SDBDU 2017.3687	RS	Μ	14.9	4.6	3.9	2.0	1.5	1.0	0.7	1.6	1.0	1.2	2.4	3.6	0.4	1.0	2.1	1.3	0.2	0.2	0.3	0.3
		Mean	16.2	5.1	3.9	2.0	1.5	1.2	0.7	1.8	1.2	1.3	2.6	3.6	0.4	1.0	2.2	1.3	0.2	0.2	0.3	0.3
		SD	1.6	0.5	0.1	0.1	0.1	0.2	0.1	0.1	0.2	0.1	0.3	0.3	0.1	0.1	0.1	0.1	0.0	0.0	0.1	0.1
Vocuher No	status	sex	FDIII	FWIII	FDIV	FWIV	ΤL	SHL	FOL	TFOL	TDI	IWI	TDII	IIMT	TDIII T	TWIII	T DIV T	TWIV	VQT	VWL	IMT	OMT
SDBDU 2017.3675	RS	М	0.4	0.4	0.3	0.3	7.7	7.9	8.8	11.9	0.3	0.3	0.4	0.4	0.5	0.4	0.5	0.4	0.5	0.5	0.5	0.4
SDBDU 2017.3689	RS	Σ	0.4	0.4	0.3	0.3	7.6	7.9	8.1	11.3	0.3	0.3	0.4	0.4	0.4	0.3	0.5	0.4	0.3	0.3	0.5	0.4
SDBDU 2017.3673	RS	Σ	0.4	0.4	0.3	0.3	7.5	7.9	8.5	11.6	0.3	0.3	0.4	0.4	0.6	0.5	0.5	0.4	0.3	0.3	0.6	0.5
SDBDU 2017.3674	RS	Μ	0.4	0.4	0.3	0.3	7.6	7.8	8.4	11.9	0.4	0.4	0.5	0.4	0.7	0.4	0.6	0.5	0.5	0.4	0.5	0.5
SDBDU 2017.3676	RS	М	0.3	0.3	0.3	0.3	7.7	7.9	8.7	11.7	0.4	0.4	0.4	0.4	0.5	0.5	0.4	0.4	0.3	0.3	0.4	0.4
SDBDU 2017.3688	RS	Μ	0.3	0.3	0.2	0.2	7.1	7.3	8.1	11.2	0.3	0.3	0.3	0.3	0.4	0.4	0.4	0.4	0.3	0.3	0.4	0.3
SDBDU 2017.3687	RS	Μ	0.3	0.3	0.3	0.3	7.3	7.5	8.2	11.0	0.2	0.2	0.3	0.3	0.4	0.4	0.4	0.4	0.3	0.3	0.5	0.3
		Mean	0.4	0.4	0.3	0.3	7.5	7.7	8.4	11.5	0.3	0.3	0.4	0.4	0.5	0.4	0.5	0.4	0.4	0.3	0.5	0.4
		SD	0.1	0.1	0.0	0.0	0.2	0.2	0.3	0.4	0.1	0.1	0.1	0.0	0.1	0.1	0.1	0.0	0.1	0.1	0.1	0.1
									Microhyla cf.	vla cf. hε	heymonsi											
Vocuher No	status	sex	SVL	МН	HL	SL	EL	EN	SN	IUE	UEW	N	FAL	HAL	FIL	FIIL	FIIIL	FIVL	FDI	FWI	FDII	FWII
WII HS 08	RS	male	20.2	6.4	5.9	2.5	1.8	1.2	0.8	2.0	1.2	1.8	4.2	5.6	1.0	1.5	3.2	1.9	0.4	0.3	0.5	0.4
Vocuher No	status	sex	FDIII	FWIII	FDIV	FWIV	$\mathbf{TL}$	SHL	FOL	TFOL	TDI	IWI	TDII	IIMT	TDIII T	TWIII	T DIV T	TWIV	TDV	TWV	IMT	OMT
WII HS 08	RS	male	0.5	0.4	0.4	0.3	11.1	12.3	12.6	17.8	0.4	0.4	0.6	0.3	0.6	0.4	0.6	0.4	0.5	0.3	0.6	0.4
									Micro.	Microhyla berdmorei	Imorei											
Vocuher No	status	sex	SVL	МН	HL	SL	EL	EN	SN	IUE	UEW	ZI	FAL	HAL	FIL	FIIL	FIII	FIVL	FDI	FWI	FDII	FWII
AD5227	RS	male	33.5	11.5	9.8	4.5	2.9	2.0	1.8	3.0	1.9	2.4	6.8	8.9	1.8	3.1	5.6	3.0	0.7	0.7	0.9	0.7
AD5243	RS	male	34.9	11.6	9.9	4.4	3.1	2.1	1.8	3.1	2.1	2.5	6.7	8.8	1.7	3.2	5.6	3.3	0.7	0.7	0.8	0.6
AD5228	RS	male	36.0	11.6	9.8	4.5	3.1	2.1	1.9	3.1	2.0	2.7	6.9	9.1	1.9	3.3	5.5	3.2	0.6	0.6	0.8	0.6
ADA 45	RS	male	33.3	11.2	9.2	4.2	2.9	2.0	1.8	2.9	1.9	2.3	6.5	9.0	1.8	3.1	5.4	3.0	0.6	0.5	0.7	0.6
A0949	RS	male	35.8	11.7	9.4	4.1	3.5	2.2	1.9	3.1	1.9	2.5	6.9	9.0	2.0	3.1	5.2	3.0	0.7	0.6	0.7	0.5
A0951	RS	male	33.9	11.1	9.5	4.1	3.1	2.1	1.7	3.1	1.9	2.3	6.8	8.8	1.9	2.9	4.9	3.0	0.7	0.6	0.7	0.6
		Mean	34.6	11.5	9.6	4.3	3.1	2.1	1.8	3.1	2.0	2.5	6.8	8.9	1.9	3.1	5.4	3.1	0.7	0.6	0.8	0.6
		SD	1.2	0.2	0.3	0.2	0.2	0.1	0.1	0.1	0.1	0.2	0.2	0.1	0.1	0.1	0.3	0.1	0.1	0.1	0.1	0.1
Vocuher No	status	sex	FDIII	FWIII	FDIV	FWIV	$\mathbf{TL}$	SHL	FOL	TFOL	TDI	IWI	TDII	TWI	TDIII T	TWIII	TDIV T	TWIV	VDV	<b>TWV</b>	IMT	OMT
A DECOT	DC	- [	¢	t		1																

0.8	0.8	0.7	0.7	0.7	0.7	0.1		FWII	0.4	0.4	0.4	0.3	0.4	0.4	0.0	OMT	0.5	0.5	0.6	0.5	0.5	0.5	0.0		FWII	0.5	0.6	0.4	0.5	0.5	0.1	OMT	0.7	0.7	0.8	0.7	0.7	0.1
1.4	1.4	1.3	1.1	1.2	1.3	0.2		FDII	0.4	0.4	0.4	0.3	0.4	0.4	0.0	IMT	0.8	0.8	0.9	0.8	0.9	0.8	0.1		FDII	0.5	0.6	0.4	0.5	0.5	0.1	IMT	0.8	0.9	1.0	1.0	0.9	0.1
0.6	0.6	0.6	0.6	0.6	0.6	0.0		FWI	0.4	0.4	0.4	0.4	0.3	0.4	0.0	TWV	0.4	0.3	0.4	0.3	0.4	0.4	0.1		FWI	0.4	0.4	0.4	0.4	0.4	0.0	TWV	0.4	0.4	0.4	0.4	0.4	0.0
1.3	1.4	1.3	1.2	1.1	1.3	0.1		FDI	0.4	0.4	0.4	0.4	0.3	0.4	0.0	TDV	0.5	0.5	0.6	0.5	0.5	0.5	0.0		FDI	0.4	0.4	0.4	0.4	0.4	0.0	VQT	0.7	0.8	0.6	0.6	0.7	0.1
0.7	0.7	0.6	0.6	0.6	0.6	0.1		FIVL	1.6	1.7	1.2	1.4	17	4.6	6.9	TWIV	0.3	0.4	0.4	0.4	0.4	0.4	0.0		FIVL	1.9	2.0	1.9	1.9	1.9	0.1	VIWT	0.4	0.4	0.4	0.4	0.4	0.0
1.7	1.6	1.2	1.3	1.3	1.4	0.2		FIIIL	2.7	3.2	2.8	2.9	2.8	2.9	0.2	TDIV	0.6	0.7	0.8	0.6	0.6	0.7	0.1		FIIIL	3.4	3.4	3.2	3.3	3.3	0.1	TDIV	0.8	0.8	0.8	0.8	0.8	0.0
0.6	0.6	0.6	0.6	0.6	0.6	0.0		FIIL	1.4	1.5	1.5	1.6	1.3	1.5	0.1	TWIII	0.3	0.4	0.4	0.3	0.4	0.4	0.1		FIIL	1.6	1.7	1.7	0.8	1.5	0.4	IIIMI	0.4	0.4	0.3	0.4	0.4	0.1
1.2	1.4	1.4	1.4	1.5	1.4	0.1		FIL	1.0	0.9	1.0	0.9	0.8	0.9	0.1	TDIII	0.6	0.7	0.7	0.6	0.6	0.6	0.1		FIL	0.8	0.9	0.9	0.8	0.9	0.1	TDIII	0.9	0.8	0.6	0.7	0.8	0.1
0.5	0.6	0.5	0.5	0.6	0.6	0.1	-	HAL	4.9	5.0	5.4	5.0	5.2	5.1	0.2	IIWI	0.3	0.4	0.4	0.3	0.4	0.4	0.1		HAL	5.4	5.2	5.5	5.5	5.4	0.1	IIWI	0.4	0.5	0.4	0.4	0.4	0.0
1.5	1.4	0.1	1.4	1.2	1.2	0.5		FAL	3.4	3.4	4.0	3.4	3.2	3.5	0.3	TDII	0.4	0.6	0.5	0.6	0.5	0.5	0.1		FAL	4.4	4.5	4.3	4.3	4.4	0.1	TDII	0.7	0.8	0.7	0.7	0.7	0.1
0.6	0.6	0.5	0.6	0.6	0.6	0.1	-	Z	1.3	1.3	1.3	1.2	1.4	1.3	0.1	TWI	0.3	0.4	0.5	0.4	0.3	0.4	0.1		Z	1.8	1.9	1.8	1.8	1.8	0.0	IWI	0.3	0.4	0.4	0.3	0.4	0.1
0.9	0.9	0.8	0.9	1.0	0.9	0.1	rapanii	UEW	1.2	1.2	1.4	1.2	1.3	1.3	0.1	TDI	0.3	0.5	0.6	0.4	0.4	0.4	0.1	hlesuri	UEW	1.2	1.2	1.3	1.3	1.3	0.1	TDI	0.5	0.5	0.5	0.5	0.5	0.0
28.3	30.2	29.3	30.4	29.6	29.6	0.8	Microhyla chakrapanii	IUE		1.9	1.8	1.9	1.9	1.9	0.0	TFOL	16.8	17.2	17.9	17.3	17.4	17.3	0.4	Microhyla mukhlesuri	IUE	2.2	2.2	2.6	2.3	2.3	0.2	TFOL	18.2	18.1	18.3	18.5	18.3	0.2
20.6	21.4	21.1	21.4	20.8	21.1	0.3	Microh	SN	0.7	0.9	0.8	0.6	0.7	0.7	0.1	FOL	11.6	11.9	11.9	11.4	11.4	11.6	0.3	Microh	SN	1.0	1.0	1.0	1.1	1.0	0.1	FOL	12.2	12.4	12.7	12.3	12.4	0.2
22.8	24.3	23.4	24.9	23.5	23.7	0.8		EN	1.4	1.4	1.3	1.3	1.5	1.4	0.1	SHL	11.4	11.8	11.9	11.5	11.2	11.6	0.3		EN	1.5	1.4	1.6	1.5	1.5	0.1	SHL	12.7	12.7	12.9	12.2	12.6	0.3
20.8	21.3	20.1	21.9	20.6	20.9	0.6		EL	1.6	1.6	1.5	1.4	1.9	1.6	0.2	TL	10.1	10.2	10.6	10.9	10.1	10.4	0.4		EL	1.6	1.7	1.8	1.9	1.8	0.1	ΤL	11.3	11.4	11.8	11.4	11.5	0.2
0.6	0.7	0.6	0.6	0.6	0.6	0.1		SL	2.4	2.6	2.6	2.4	2.4	2.5	0.1	FWIV	0.4	0.4	0.5	0.4	0.4	0.4	0.0		SL	2.9	3.0	3.1	3.0	3.0	0.1	FWIV	0.5	0.5	0.5	0.5	0.5	0.0
0.7	0.8	0.8	0.7	0.7	0.8	0.1		HL	4.5	4.4	4.8	4.6	4.9	4.6	0.2	FDIV	0.4	0.4	0.5	0.4	0.4	0.4	0.0		HL	5.6	5.8	5.8	5.7	5.7	0.1	FDIV	0.5	0.5	0.5	0.5	0.5	0.0
0.6	0.7	0.7	0.8	0.7	0.7	0.1		MH	5.9	5.6	6.1	5.5	6.2	5.9	0.3	FWIII	0.4	0.4	0.5	0.4	0.4	0.4	0.0		МH	6.7	6.7	6.9	6.8	6.8	0.1	FWIII	0.6	0.6	0.5	0.5	0.6	0.1
0.8	1.0	0.8	1.0	0.8	0.9	0.1		SVL	17.9	20.3	22.2	19.8	21.2	20.3	1.6	FDIII	0.4	0.4	0.5	0.4	0.4	0.4	0.0		SVL	23.8	23.9	24.8	24.3	24.2	0.5	FDIII	0.6	0.6	0.5	0.5	0.6	0.1
male	male	male	male	male	Mean	SD		sex	male	male	male	male	male	Mean	SD	sex	male	male	male	male	male	Mean	SD		sex	male	male	male	male	Mean	SD	sex	male	male	male	male	Mean	SD
RS	RS	RS	RS	RS				status	RS	RS	RS	RS	RS			status	RS	RS	RS	RS	RS				status	RS	RS	RS	RS			status	RS	RS	RS	RS		
AD5243	AD5228	ADA 45	A0949	A0951				Vocuher No	WII HC 185	WII HC 095	WII HC 184	WII HC 112	WII HC 010			Vocuher No	WII HC 185	WII HC 095	WII HC 184	WII HC 112	WII HC 010				Vocuher No	SDBDU 2010.1333	SDBDU 2010.20	SDBDU 2010.132B	SDBDU 2010.21			Vocuher No	SDBDU 2010.1333	SDBDU 2010.20	SDBDU 2010.132B	SDBDU 2010.21		

9.0	0.5	0.7	0.5	0.6	0.5	0.6	0.1		FWII	0.4	0.4	0.5	0.4	0.4	0.3	0.4	0.1	OMT	0.4	0.5	0.4	0.6	0.4	0.4	0.5	0.1		FWII	0.4	0.5	0.5	0.5	0.4	0.5	0.5	0.4	0.4	0.5	0.1
6.0	0.6	0.7	0.6	0.6	0.6	0.8	0.2	-	FDII	0.4	0.4	0.5	0.4	0.4	0.3	0.4	0.1	IMT	0.6	0.5	0.6	0.7	0.6	0.6	0.6	0.1		FDII	0.4	0.5	0.5	0.5	0.4	0.5	0.5	0.4	0.4	0.5	0.1
0.5	0.4	0.5	0.4	0.5	0.4	0.4	0.1		FWI	0.3	0.4	0.4	0.4	0.4	0.3	0.4	0.1	TWV	0.5	0.5	0.5	0.5	0.4	0.5	0.5	0.0		FWI	0.4	0.5	0.5	0.4	0.5	0.4	0.4	0.4	0.4	0.4	0.1
0.5	0.4	0.5	0.4	0.5	0.4	0.4	0.0	-	FDI	0.3	0.4	0.4	0.4	0.4	0.3	0.4	0.1	TDV	0.5	0.5	0.5	0.5	0.4	0.5	0.5	0.0		FDI	0.4	0.5	0.5	0.4	0.5	0.4	0.4	0.4	0.4	0.4	0.1
0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.0		FIVL	1.9	2.1	1.9	1.8	1.6	1.7	1.8	0.2	TWIV	0.5	0.5	0.7	0.5	0.4	0.5	0.5	0.1		FIVL	1.8	1.9	1.9	1.6	1.8	1.7	1.6	1.5	1.2	1.7	0.2
0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.0		FIIIL	3.2	3.5	3.6	3.2	2.9	3.0	3.2	0.3	VIUT	0.5	0.5	0.7	0.5	0.4	0.5	0.5	0.1		FIIIL	3.7	3.8	3.9	3.7	3.9	3.7	3.5	3.8	3.2	3.7	0.2
0.5	0.4	0.4	0.4	0.4	0.4	0.4	0.1	-	FIIL	1.5	1.8	1.7	1.8	1.4	1.4	1.6	0.2	IIIMT	0.5	0.5	0.6	0.5	0.4	0.4	0.5	0.1		FIIL	1.8	1.8	1.7	1.7	1.8	1.7	1.8	1.7	1.6	1.7	0.1
0.5	0.4	0.4	0.4	0.4	0.4	0.4	0.1	-	FIL	0.9	1.0	1.0	0.9	0.7	0.9	0.9	0.1	TDII	0.5	0.5	0.6	0.5	0.4	0.4	0.5	0.1		FIL	0.7	0.8	0.8	0.7	0.9	0.8	0.7	0.8	0.6	0.8	0.1
0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.1		HAL	5.3	5.6	5.7	5.7	5.1	4.7	5.4	0.4	IIWI	0.4	0.5	0.5	0.5	0.4	0.4	0.5	0.1		HAL	6.0	6.1	6.4	6.5	6.9	6.3	5.9	6.5	5.6	6.2	0.4
0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.1	-	FAL	3.7	3.9	4.2	4.1	4.1	3.3	3.9	0.3	TDI	0.4	0.5	0.5	0.5	0.4	0.4	0.5	0.1		FAL	5.1	5.0	4.9	4.5	5.0	4.9	4.8	5.0	4.6	4.9	0.2
0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.0		Z	1.3	1.3	1.4	1.3	1.4	1.3	1.3	0.1	IWI	0.4	0.4	0.5	0.4	0.4	0.3	0.4	0.1		Z	1.8	1.9	2.0	2.0	2.0	2.0	1.7	2.0	1.5	1.9	0.2
0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.0	nilphamariensis	UEW	1.3	1.3	1.3	1.3	1.3	1.2	1.3	0.0	TDI	0.4	0.4	0.5	0.4	0.4	0.3	0.4	0.1	ntalei	UEW	1.5	1.6	1.9	1.9	2.1	2.0	1.6	1.9	1.3	1.8	0.3
14.0	11.7	13.4	12.1	13.7	12.7	13.4	0.9		IUE	1.9	2.1	2.1	2.4	1.9	1.8	2.0	0.2	TFOL	14.2	15.5	16.4	15.5	13.1	13.1	14.6	1.4	Microhyla mihintalei	IUE	2.6	3.0	2.9	3.0	3.3	2.8	1.6	2.6	2.2	2.7	0.5
9.8	8.4	9.3	8.6	9.7	8.7	9.3	0.5	Microhyla	SN	0.7	0.8	0.8	0.7	0.7	0.8	0.8	0.1	FOL 7	12.3	11.2	11.2	10.7	9.9	9.8	10.9	0.9	Microh	SN	1.0	1.0	1.3	1.4	1.6	1.2	1.0	1.2	1.0	1.2	0.2
10.7	9.2	9.7	8.8	9.8	9.1	9.8	0.6	W	EN	1.2	1.4	1.4	1.3	1.2	1.2	1.3	0.1	SHL	10.0	10.3	10.1	10.1	8.7	9.1	9.7	0.7		EN	1.4	1.5	1.7	1.6	1.7	1.6	1.5	1.5	1.4	1.5	0.1
9.7	8.5	9.2	8.2	9.5	8.2	9.0	0.7	-	EL	1.6	1.9	2.0	1.8	1.7	1.6	1.8	0.2		10.1	10.3	10.0	10.1	8.9	9.0	9.7	0.6		EL	2.3	2.4	2.5	2.6	2.8	2.5	2.4	2.5	2.1	2.5	0.2
0.3	0.4	0.4	0.4	0.4	0.4	0.4	0.0		SL	2.7	2.7	2.9	2.7	2.3	2.2	2.6	0.3	FWIV	0.4	0.4	0.5	0.4	0.4	0.3	0.4	0.1		SL	2.7	2.9	3.0	2.9	3.0	2.8	2.6	2.7	2.5	2.8	0.2
0.3	0.4	0.4	0.4	0.4	0.4	0.4	0.0	-	HL	5.1	5.4	5.2	5.1	5.1	5.8	5.3	0.3	FDIV 1	0.4	0.4	0.5	0.4	0.4	3.0	0.0	1.1		HL	6.2	6.4	6.7	6.5	6.7	6.6	5.6	6.1	5.0	6.2	0.6
0.4	0.5	0.5	0.4	0.4	0.4	0.4	0.0		МH	6.5	6.3	6.6	6.0	6.1	6.3	6.3	0.2	FWIII	0.4	0.5	0.5	0.4	0.4	0.4	0.4	0.1		ΗW	7.4	7.6	8.1	7.9	8.1	8.0	7.2	8.0	6.9	7.7	0.4
0.4	0.5	0.5	0.4	0.4	0.4	0.4	0.0	-	SVL	23.8	23.1	23.1	21.3	19.5	19.3	21.7	2.0	FDIII	0.4	0.5	0.5	0.4	0.4	0.4	0.4	0.1		SVL	24.8	25.8	26.7	26.4	27.3	26.1	24.3	26.7	21.7	25.5	1.7
male	male	male	male	male	male	Mean	SD	-	sex	male	male	male	male	male	male	Mean	SD	sex	male	male	male	male	male	male	Mean	SD		sex	male	Mean	SD								
RS	RS	RS	RS	RS	RS	-		-	status	RS	RS	RS	RS	RS	RS			status	RS	RS	RS	RS	RS	RS				status	HT		ΡT	PT	PT	ΡT	ΡT	ΡT	ΡT		
SDBDU 2012.2198	DZ 1432	DZ 1052	DZ 1471	DZ 1085	DZ 1104				Vocuher No s	SDBDU 2011.586	SDBDU 2010.349	SDBDU 2014.2482	SDBDU 2015.3060	ADM 017	SDBDU 2015.3121			Vocuher No s	SDBDU 2011.586	SDBDU 2010.349	SDBDU 2014.2482	SDBDU 2015.3060	ADM 017	SDBDU 2015.3121				Vocuher No s	DZ 1553	DZ 1554	DZ 1555	DZ 1556	DZ 1557	DZ 1467	DZ 1468	DZ 1473	DZ 1410		

FDIII FWIII FDIV FWIV 1
C.11 C.11 +.0 +.0 C.0 C.0 20 20 20
male 0.2 0.2 0.2 0.3 12.4 11.3 12.4 11.3 male 0.4 0.4 0.4 0.4 1.2 1.2 12.4 12.1
0.5 0.5 0.5 0.5 12.5
male 0.5 0.5 0.5 0.5 12.1 12.3
male 0.5 0.5 0.4 0.4 11.1 11.2
0.4
male 0.4 0.5 0.5 10.8 10.9
Mean 0.5 0.5 0.5 0.5 11.7 11.9
SD 0.1 0.1 0.1 0.1 0.6 0.6
sex SVL HW HL SL EL EN
male 27.9 8.1 6.7 3.6 2.6 1.6
male 24.8 8.3 7.1 3.4 2.2 1.7
male 27.9 8.2 8.2 3.2 2.4 1.8
9.2 7.1 2.9
male 29.6 9.2 7.1 2.9 3.0 1.7
male 28.4 8.7 7.1 3.1 2.6 1.5
male 27.2 8.2 6.8 3.0 2.7 1.4
male 25.8 7.4 6.9 2.7 2.2 1.6
Mean 27.6 8.4 7.1 3.1 2.6 1.6
SD 1.6 0.6 0.5 0.3 0.3 0.1
sex FDIII FWIII FDIV FWIV TL SHI
male 0.5 0.5 0.5 0.5 14.3 12.1
male 0.5 0.5 0.5 0.5 14.1 12.0
male 0.5 0.5 0.5 0.5 13.0 12.1
male 0.5 0.5 0.5 0.5 14.3 12.2
male 0.5 0.5 0.5 0.5 14.3 12.2
male 0.5 0.5 0.5 0.5 13.6 12.0
male 0.5 0.5 0.5 0.5 12.0 12.4
male 0.5 0.5 0.4 0.4 12.0 11.9
Mean 0.5 0.5 0.5 0.5 13.5 12.1
SD 0.0 0.0 0.0 0.0 1.0 0.2
-
sex SVL HW HL SL EL
male 15.1 4.3 4.1 1.9 1.3 0.9
male 15.2 4.6 4.3 1.9 1.4 1.0

		male	4.01	4./	4.5	2.0	1.4	V.Y	0. /	0.1	0.7	C.1	t. 1	0.0	0./	1.3	7.7	1.4	0.3	0.3	c.u	7.0
ZSI/WGRC/V/A/964	ΡT	male	15.4	4.2	3.9	1.9	1.3	0.9	0.7	1.7	0.9	1.2	2.6	3.8	0.8	1.2	2.3	1.3	0.3	0.3	0.3	0.3
ZSI/WGRC/V/A/965	PT	male	15.0	4.1	4.0	1.9	1.3	0.9	0.7	1.5	0.7	1.0	2.4	3.9	0.6	1.1	2.2	1.2	0.3	0.2	0.3	0.2
SDBDU 2015.2976	RS	male	15.7	4.9	4.4	2.1	1.5	1.0	0.8	1.9	0.9	1.2	2.5	4.1	0.7	1.2	2.0	1.5	0.3	0.3	0.3	0.3
		Mean	15.3	4.5	4.2	2.0	1.4	0.9	0.7	1.7	0.8	1.2	2.4	3.9	0.7	1.3	2.3	1.4	0.3	0.3	0.3	0.3
		SD	0.3	0.3	0.2	0.1	0.1	0.1	0.0	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.0	0.1	0.0	0.1
Vocuher No st	status	sex	FDIII	FWIII	FDIV	FWIV	TL	SHL	FOL	TFOL	IOI	IWI	IIQI	IIMT	TDII	IIIMT	TDIV	VIWT	VUT	TWV	IMT	OMT
ZSI/WGRC/V/A/961	HT	male	0.4	0.3	0.3	0.3	7.3	8.3	8.0	11.8	0.4	0.4	0.5	0.4	0.6	0.4	0.6	0.3	0.5	0.3	0.6	0.3
	PT	male	0.4	0.3	0.3	0.3	7.5	8.4	8.2	11.9	0.4	0.4	0.4	0.4	0.6	0.4	0.6	0.5	0.6	0.5	0.5	0.2
	ΡT	male	0.4	0.3	0.3	0.3	7.4	8.1	7.9	11.6	0.3	0.3	0.4	0.3	0.5	0.3	0.5	0.4	0.4	0.4	0.5	0.2
ZSI/WGRC/V/A/964	PT	male	0.4	0.3	0.4	0.3	7.5	8.2	8.0	11.7	0.3	0.3	0.5	0.4	0.6	0.4	0.6	0.4	0.5	0.4	0.5	0.2
ZSI/WGRC/V/A/965	ΡT	male	0.3	0.2	0.3	0.2	7.6	8.2	8.0	11.0	0.3	0.3	0.4	0.2	0.6	0.3	0.6	0.3	0.5	0.3	0.4	0.2
SDBDU 2015.2976	RS	male	0.4	0.3	0.4	0.3	7.6	8.2	8.0	12.1	0.4	0.4	0.4	0.4	0.5	0.4	0.6	0.4	0.6	0.05	0.5	0.3
	1	Mean	0.4	0.3	0.3	0.3	7.5	8.2	8.0	11.7	0.4	0.4	0.4	0.4	0.6	0.4	0.6	0.4	0.5	0.3	0.5	0.2
		SD	0.0	0.0	0.1	0.0	0.1	0.1	0.1	0.4	0.1	0.1	0.1	0.1	0.1	0.1	0.0	0.1	0.1	0.2	0.1	0.1
									Microhy	Microhyla karunaratnei	ıaratnei											
Vocuher No st	status	sex	SVL	HW	HL	SL	EL	EN	NS	IUE	UEW	N	FAL	HAL	FIL	FIIL	FIIL	FIVL	FDI	FWI	FDII	FWII
		male	13.8	4.9	4.1	1.8	1.4	1.3	0.6	1.6	0.7	0.9	3.7	2.9	0.6	0.9	2.1	1.0	0.2	0.2	0.3	0.2
DZ 1530		male	15.1	5.5	4.8	2.0	1.5	1.5	0.8	2.1	0.9	1.3	4.1	3.4	0.8	1.1	2.4	1.1	0.2	0.2	0.3	0.2
DZ 1529	RS	male	14.8	5.4	4.9	1.9	1.6	1.2	0.7	1.7	0.9	1.2	4.0	3.4	0.7	1.0	2.3	1.1	0.2	0.2	0.3	0.2
		Mean	14.6	5.3	4.6	1.9	1.5	1.3	0.7	1.8	0.8	1.1	3.9	3.2	0.7	1.0	2.3	1.1	0.2	0.2	0.3	0.2
		SD		0.3	0.4	0.1	0.1	0.2	0.1	0.3	0.1	0.2	0.2	0.3	0.1	0.1	0.2	0.1	0.0	0.0	0.0	0.0
Vocuher No st	status	sex	FDIII	FWIII	FDIV	FWIV	$\mathbf{TL}$	SHL	FOL	TFOL	TDI	TWI	TDII	TWI	TDIII 1	TWIII	TDIV	TWIV	TDV	TWV	IMT	OMT
DZ 1531	RS	male	0.3	0.2	0.3	0.2	7.1	7.8	7.6	11.2	0.3	0.2	0.5	0.3	0.6	0.5	0.5	0.3	0.4	0.3	0.4	0.3
		male	0.4	0.3	0.3	0.2	7.3	8.2	8.3	12.0	0.4	0.3	0.6	0.4	0.6	0.5	0.6	0.4	0.4	0.3	0.5	0.4
1529	RS	male	0.4	0.2	0.3	0.2	7.0	8.2	8.2	11.8	0.4	0.3	0.5	0.3	0.6	0.5	0.6	0.4	0.4	0.3	0.5	0.4
	_	Mean	0.4	0.2	0.3	0.2	7.1	8.1	8.0	11.7	0.4	0.3	0.5	0.3	0.6	0.5	0.6	0.4	0.4	0.3	0.5	0.4
	_	SD	0.1	0.1	0.0	0.0	0.2	0.2	0.4	0.4	0.1	0.1	0.1	0.1	0.0	0.0	0.1	0.1	0.0	0.0	0.1	0.1
-									Micr	Microhyla lat	laterite											
	status	sex	SVL	ΜH	HL	SL	EL	EN	SN	IUE	UEW	Z	FAL	HAL	FIL	FIIL	FIIIL	FIVL	FDI	FWI	FDII	FWII
		male	16.1	4.8	4.3	2.1	1.4	0.9	0.7	1.7	1.0	1.2	2.9	3.9	0.8	1.4	2.2	1.2	0.3	0.3	0.3	0.3
	RS	male	16.2	4.6	4.2	2.3	1.3	1.0	0.9	1.8	0.9	1.2	2.8	3.7	0.8	1.2	2.0	1.4	0.3	0.3	0.3	0.3
	RS	male	15.4	4.3	4.0	2.0	1.4	0.8	0.7	1.5	0.8	1.1	2.8	3.8	0.6	1.3	2.3	1.4	0.3	0.3	0.4	0.3
SDBDU 2015.3066	RS	male	15.4	4.6	4.3	2.3	1.3	0.8	0.8	1.8	0.9	1.2	2.9	3.9	0.9	1.5	2.6	1.3	0.3	0.3	0.4	0.3
SDBDU 2015.3067	RS	male	14.3	4.2	3.8	1.8	1.2	0.8	0.6	1.4	0.7	1.1	2.7	3.3	0.6	1.1	2.1	1.2	0.2	0.2	0.3	0.3
	-	Mean	15.5	4.5	4.1	2.1	1.3	0.9	0.7	1.6	0.9	1.2	2.8	3.7	0.7	1.3	2.2	1.3	0.3	0.3	0.3	0.3
		SD	0.8	0.2	0.2	0.2	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.2	0.1	0.2	0.2	0.1	0.0	0.0	0.1	0.0
	status	sex	FDIII	FWIII	FDIV	FWIV	$\mathbf{TL}$	SHL	FOL	TFOL	TDI	TWI	TDII	IIMI	TDIII 1	IIIMI	TDIV	TWIV	TDV	TWV	IMT	OMT
SDBDU 2015.3062	RS	male	0.4	0.4	0.4	0.4	7.9	8.6	8.3	11.7	0.4	0.4	0.5	0.4	0.6	0.4	0.6	0.4	0.5	0.3	0.6	0.6
	1	,																				

								Micr	Microhyla laterite	erite										
IS SEX FDIII FWIII FDIV FWIV TL	FWIII FDIV FWIV TL	FWIII FDIV FWIV TL	FDIV FWIV TL	TL	-	2	SHL	7	TFOL	IUI	_†	IIDII	_	_	∃	>	>	AMT AGT	-	
RS male 0.5 0.3 0.5 0.3 7.8 8.4	0.5 0.3 0.5 0.3 7.8	0.3 0.5 0.3 7.8	0.3 7.8	7.8		8.4		8.4	11.1	0.3	0.3	0.5	0.3	0.6	0.3	0.7 0	0.4 0.	0.6 0.3	9.0	0.4
RS male 0.4 0.3 0.4 0.3 7.9 8.9	0.4 0.3 0.4 0.3 7.9	0.3 0.4 0.3 7.9	0.3 7.9	7.9		8.9	_	8.6	11.8	0.4	0.4	0.6	0.4	0.7	0.3	0.7 0	0.3 0.	0.6 0.3	9.0	0.5
RS male 0.4 0.3 0.3 0.3 7.0 7.9	0.4 0.3 0.3 0.3 7.0	0.3 0.3 0.3 7.0	0.3 7.0	7.0		7.9	_	7.4	10.6	0.3	0.2	0.4	0.3	0.5	0.3	0.5 0	0.4 0	0.4 0.3	9.4	0.3
Mean         0.4         0.3         0.4         0.3         7.7         8.5	0.4 0.3 0.4 0.3 7.7	0.3 0.4 0.3 7.7	0.3 7.7	7.7		8	2	8.3	11.4	0.4	0.3	0.5	0.3	0.6	0.3	0.6 0	0.4 0.	0.5 0.3	0.5	0.4
SD 0.1 0.1 0.1 0.1 0.4 0.4	0.1 0.1 0.1 0.4	0.1 0.1 0.1 0.4	0.1 0.4	0.4	4	0.4	_	0.5	0.5	0.1	0.1	0.1	0.1	0.1	0.1	0.1 0	0.0	0.1 0.0	0.1	0.1
		-			-			Micro	Microhyla sholigari	ligari			-	-	-	-	-		-	-
status sex SVL HW HL SL EL	HW HL SL E	HW HL SL E	SLE	E	EL		EN	NS	IUE	UEW	N	FAL	HAL ]	FIL	FIIL F	FIIIL FI	FIVL FDI	DI FW	T FDII	FWII
RS male 18.0 4.8 4.3 2.3 1.7	18.0 4.8 4.3 2.3	4.8 4.3 2.3	2.3		1.7	1	1.1	0.8	1.8	1.1	1.1	3.5	4.5	1.1	1.6	2.9 1	7 0.	0.4 0.4	1 0.4	0.4
RS male 17.2 4.7 4.1 2.3 1.6	17.2 4.7 4.1 2.3	4.7 4.1 2.3	2.3		1.6	-	0.9	0.7	1.7	1.0	1.1	3.2	4.4	0.9	1.5	2.7 1	1.6 0.	0.3 0.3	9.4	0.4
RS male 16.9 4.7 4.0 2.1 1.6	16.9 4.7 4.0 2.1	4.7 4.0 2.1	2.1		1.6		0.9	0.7	1.7	1.0	1.1	3.3	4.3	1.1	1.6	2.7 1	1.6 0.	0.3 0.3	9.4	0.3
RS male 17.1 4.7 4.1 2.3 1.7	17.1 4.7 4.1 2.3	4.7 4.1 2.3	2.3		1.7		0.9	0.8	1.8	1.1	1.1	3.5	4.4	1.0	1.6	2.8 1	1.6 0.	0.4 0.4	1 0.3	0.3
RS male 16.5 4.7 4.1 2.1 1.5	16.5 4.7 4.1 2.1	4.7 4.1 2.1	2.1		1.5		0.9	0.7	1.7	0.9	1.1	3.1	4.2	0.9	1.5	2.6 1	1.6 0.	0.3 0.3	3 0.3	0.3
Mean 17.1 4.7 4.1 2.2 1.6	17.1 4.7 4.1 2.2	4.7 4.1 2.2	2.2		1.6		0.9	0.7	1.7	1.0	1.1	3.3	4.4	1.0	1.6	2.7 1	1.6 0.	0.3 0.3	9.4	0.3
SD 0.6 0.0 0.1 0.1 0.1	0.6 0.0 0.1 0.1	0.0 0.1 0.1	0.1		0.1		0.1	0.1	0.1	0.1	0.0	0.2	0.1	0.1	0.1	0.1 0	0.0	0.1 0.1	0.1	0.1
status sex FDIII FWIII FDIV FWIV TL	FDIII FWIII FDIV FWIV T	FWIII FDIV FWIV T	FDIV FWIV T	T	ΤΓ	-	SHL	FOL	TFOL	TDI	IWT	TDII	TWII T	TDIII T	TWIII T	TDIV TV	TWIV TI	TDV TWV	TMI V	TMO .
RS male 0.5 0.4 0.4 8.4	0.5 0.4 0.4 0.4 8.	0.4 0.4 0.4 8.	0.4 8.	8.	8.4		9.3	9.5	13.4	0.4	0.4	0.5	0.3	0.6	0.3	0.7 0	0.4 0	0.5 0.3	3 0.7	0.5
RS male 0.3 0.3 0.4 0.4 8.0	0.3 0.3 0.4 0.4 8.	0.3 0.4 0.4 8.	0.4 8.	8.	8.0		8.8	8.8	12.9	0.4	0.3	0.5	0.3	0.5	0.3	0.6 0	0.4 0	0.5 0.3	9.7	0.4
RS male 0.4 0.3 0.4 0.3 8.6	0.4 0.3 0.4 0.3 8.	0.3 0.4 0.3 8.	0.3 8.	8.	8.6		9.5	9.0	13.1	0.5	0.4	0.5	0.3	0.6	0.3	0.7 0	0.4 0.	0.5 0.3	0.7	0.5
RS male 0.4 0.3 0.4 0.4 8.3	0.4 0.3 0.4 0.4 8.	0.3 0.4 0.4 8.	0.4 8.	.8	8.3		9.6	9.2	13.1	0.4	0.4	0.4	0.3	0.6	0.4	0.6 0	0.3 0.	0.5 0.3	0.7	0.4
RS male 0.4 0.3 0.4 0.3 8.4	0.4 0.3 0.4 0.3 8.	0.3 0.4 0.3 8.	0.3 8.	8.	8.4		9.0	9.0	13.2	0.4	0.3	0.5	0.4	0.6	0.4	0.6 0	0.3 0.	0.5 0.3	0.7	0.4
Mean 0.4 0.3 0.4 0.4 8.3	0.4 0.3 0.4 0.4 8.	0.3 0.4 0.4 8.	0.4 8.	×.	8.3		9.2	9.1	13.1	0.4	0.4	0.5	0.3	0.6	0.3	0.6 0	0.4 0.	0.5 0.3	0.7	0.4
SD 0.1 0.0 0.0 0.1 0.2	0.0 0.0 0.1 0.	0.0 0.0 0.1 0.	0.1 0.	0.			0.3	0.3	0.2	0.0	0.1	0.0	0.0	0.0	0.1	0.1 0	0.1 0.	0.0 0.0	0.0	0.1
								Micro	Microhyla zeylanica	anica										
status sex SVL HW HL SL EL	HW HL SL E	HW HL SL E	SL E	E	EL		EN	SN	IUE	UEW	Z	FAL	HAL	FIL	FIIL F	FIIIL FI	FIVL FDI	DI FW	T FDII	FWII
HT male 17.3 5.2 5.1 2.2 1.9	17.3 5.2 5.1 2.2	5.2 5.1 2.2	2.2		1.9		0.8	0.8	2.4	0.9	1.5	3.9	4.8	0.8	1.4	2.5 1	1.3 0.	0.4 0.3	9.4	0.3
RS male 17.6 5.4 5.2 2.3 1.6	17.6 5.4 5.2 2.3	5.4 5.2 2.3	2.3		1.6		0.7	0.8	2.3	0.8	1.4	3.4	4.6	0.7	1.5	2.6 1	1.4 0.	0.4 0.3	9.4	0.3
male 17.8 5.3 5.2	17.8 5.3 5.2 2.0	5.3 5.2 2.0	2.0		1.6		0.7	0.8	1.8	0.7	1.5	3.4	4.5	0.8	1.6	2.6 1	1.4 0.	0.3 0.3	9.4	0.3
RS male 19.3 5.6 5.7 2.2 2.1	19.3 5.6 5.7 2.2	5.6 5.7 2.2	2.2		2.1		0.9	0.9	2.6	1.0	1.6	3.8	4.9	0.9	1.6	2.7 1	1.5 0.	0.4 0.3	9.4	0.3
Mean 18.0 5.4 5.3 2.2 1.8	18.0 5.4 5.3 2.2	5.4 5.3 2.2	2.2	_	1.8	_	0.8	0.8	2.3	0.9	1.5	3.6	4.7	0.8	1.5	2.6 1	1.4 0.	0.4 0.3	9.4	0.3
SD 0.9 0.2 0.3 0.1 0.2	0.9 0.2 0.3 0.1	0.2 0.3 0.1	0.1		0.2		0.1	0.1	0.3	0.1	0.1	0.3	0.2	0.1	0.1	0.1 0	0.1 0.	0.1 0.0	0.0	0.0
status sex FDIII FWIII FDIV FWIV TL	FDIII FWIII FDIV FWIV T	FWIII FDIV FWIV T	FDIV FWIV T	H	ΤL		SHL	FOL	TFOL	TDI	IWT	TDII	T IIWI	TDIII T	T IIIWT	TDIV TV	TWIV TI	TDV TWV	TMI V	OMT
HT male 0.5 0.4 0.5 0.3 7.8	0.5 0.4 0.5 0.3	0.4 0.5 0.3	0.3		7.8		8.3	9.8	13.6	0.4	0.3	0.5	0.4	0.6	0.3	0.6 0	0.4 0.	0.6 0.4	1 0.5	0.4
RS male 0.5 0.3 0.5 0.3 7.9	0.5 0.3 0.5 0.3	0.3 0.5 0.3	0.3		7.9	-	8.5	9.5	12.9	0.4	0.4	0.5	0.3	0.6	0.3	0.6 0	0.4 0.	0.5 0.3	3 0.5	0.4
RS male 0.5 0.4 0.5 0.3 7.9	0.5 0.4 0.5 0.3	0.4 0.5 0.3	0.3		7.9		8.3	9.2	13.0	0.4	0.3	0.5	0.4	0.5	0.3	0.6 0	0.3 0.	0.6 0.3	9.0	0.4
RS male 0.5 0.3 0.5 0.3 8.1	0.5 0.3 0.5 0.3	0.3 0.5 0.3	0.3		8.1		8.8	9.9	13.8	0.4	0.3	0.5	0.3	0.6	0.3	0.6 0	0.4 0	0.6 0.3	9.0	0.3
Mean 0.5 0.4 0.5 0.3 7.9	0.5 0.4 0.5 0.3	0.4 0.5 0.3	0.3		7.9	⊢ –	8.5	9.6	13.3	0.4	0.3	0.5	0.4	0.6	0.3	0.6 0	0.4 0.	0.6 0.3	9.0	0.4
SD 0.0 0.1 0.0 0.0 0.1	0.1 0.0 0.0	0.1 0.0 0.0	0.0		0.1		0.2	0.3	0.4	0.0	0.0	0.0	0.1	0.1	0.0	0.0 0	0.1 0.	0.1 0.0	0.1	0.0

								Sou	theast a	nd East	Southeast and East Asian species	scies										
									Micr	Microhyla achatina	hatina											
Vocuher No	status	sex	SVL	ΜH	HL	SL	EL	EN	SN	IUE	UEW	Z	FAL	HAL	FIL	FIIL	FIIIL	FIVL	FDI	FWI	FDII	FWII
UIMZ 0031	RS	М	21.5	5.6	5.0	3.0	1.8	1.7	1.5	2.3	1.0	2.0	3.5	5.4	0.8	1.3	3.2	2.0	0.4	0.4	0.5	0.4
<b>UIMZ 0032</b>	RS	Μ	21.2	5.5	4.8	2.9	1.7	1.6	1.3	2.5	1.1	1.9	3.5	5.5	0.9	1.4	3.4	2.1	0.3	0.3	0.5	0.4
<b>UIMZ 0033</b>	RS	Μ	21.1	5.4	4.8	3.0	1.8	1.7	1.3	2.2	1.1	1.8	3.2	4.9	0.9	1.3	3.1	2.1	0.4	0.4	0.6	0.4
UIMZ 0034	RS	Μ	21.2	5.7	5.0	3.0	1.7	1.5	1.2	2.4	1.1	1.8	3.5	5.3	0.8	1.3	3.0	2.0	0.4	0.4	0.5	0.4
UIMZ 0035	RS	Σ	22.3	5.9	5.2	3.2	1.8	1.5	1.2	2.6	1.2	2.0	3.6	5.4	0.8	1.3	3.5	2.1	0.4	0.4	0.6	0.4
UIMZ 0035b	RS	Σ	22.0	5.7	5.3	3.2	1.8	1.4	1.2	2.5	1.2	2.1	3.7	5.6	0.9	1.4	3.6	2.2	0.4	0.4	0.6	0.5
		Mean	21.6	5.6	5.0	3.1	1.8	1.6	1.3	2.4	1.1	1.9	3.5	5.4	0.9	1.3	3.3	2.1	0.4	0.4	0.6	0.4
		SD	0.5	0.2	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.2	0.1	0.1	0.2	0.1	0.0	0.0	0.1	0.0
Vocuher No	status	sex	FDIII	FWIII	FDIV	FWIV	ΤL	SHL	FOL	TFOL	TDI	TWI	TDII	IIML	TDII	TWIII	TDIV	TWIV	<b>TDV</b>	VWT	IMT	OMT
UIMZ 0031	RS	Σ	0.7	0.4	9.0	0.4	11.9	13.4	12.8	18.1	0.6	0.5	0.9	0.5	1.1	0.6	1.1	0.6	1.0	0.6	0.7	0.4
UIMZ 0032	RS	Σ	0.7	0.5	0.5	0.4	11.7	13.1	12.4	17.9	0.6	0.5	1.0	0.5	1.0	0.5	1.1	0.6	0.9	0.5	0.6	0.4
UIMZ 0033	RS	Μ	0.7	0.5	0.6	0.4	11.1	12.7	12.1	17.9	0.5	0.4	0.9	0.4	1.0	0.5	1.1	0.6	1.0	0.6	0.6	0.3
UIMZ 0034	RS	Σ	0.8	0.4	0.5	0.4	11.3	13.3	12.4	18.4	0.5	0.4	1.0	0.5	1.0	0.5	1.0	0.5	1.0	0.6	0.6	0.3
UIMZ 0035	RS	Μ	0.8	0.5	0.6	0.4	11.8	13.1	12.5	18.1	0.6	0.5	1.1	0.6	1.1	0.5	1.0	0.5	1.0	0.6	0.7	0.4
UIMZ 0035b	RS	Μ	0.8	0.5	0.6	0.4	11.9	13.3	12.7	18.6	0.6	0.5	1.0	0.5	1.1	0.5	1.1	0.5	0.9	0.5	0.7	0.4
		Mean	0.8	0.5	0.6	0.4	11.6	13.2	12.5	18.2	9.6	0.5	1.0	0.5	1.1	0.5	1.1	0.6	1.0	0.6	0.7	0.4
		SD	0.1	0.1	0.1	0.0	0.3	0.3	0.2	0.3	0.1	0.1	0.1	0.1	0.1	0.0	0.1	0.1	0.1	0.1	0.1	0.1
									Micr	Microhyla m	mixtura											
Vocuher No	status	sex	SVL	ΗW	HL	SL	EL	EN	SN	IUE	UEW	Z	FAL	HAL	FIL	FIIL	FIIIL	FIVL	FDI	FWI	FDII	FWII
CIB 65706	RS	male	22.7	6.7	5.5	3.1	2.1	1.5	1.2	2.7	1.5	1.8	3.8	5.5	1.0	1.6	3.0	1.7	0.4	0.4	0.5	0.5
CIB 65696	RS	male	21.7	6.1	5.1	2.8	1.9	1.5	1.0	2.4	1.3	1.7	4.0	5.7	1.1	1.7	3.2	1.9	0.5	0.5	0.5	0.5
CIB 65692	RS	male	17.7	5.6	4.4	2.6	1.6	1.3	0.9	2.3	1.1	1.4	3.4	4.9	0.9	1.6	2.8	1.7	0.4	0.4	0.5	0.5
CIB 65701	RS	male	21.5	6.6	5.3	2.7	1.9	1.4	1.0	2.4	1.4	1.8	4.0	5.4	1.0	1.7	3.0	1.9	0.4	0.4	0.4	0.4
CIB 65691	RS	male	18.6	5.5	4.9	2.7	1.7	1.4	1.0	2.4	1.3	1.5	3.6	5.0	1.0	1.5	3.0	1.7	0.4	0.4	0.4	0.4
		Mean	20.4	6.1	5.0	2.8	1.8	1.4	1.0	2.4	1.3	1.6	3.8	5.3	1.0	1.6	3.0	1.8	0.4	0.4	0.5	0.5
		SD	2.2	0.6	0.4	0.2	0.2	0.1	0.1	0.2	0.1	0.2	0.3	0.3	0.1	0.1	0.1	0.1	0.0	0.0	0.1	0.1
Vocuher No	status	sex	FDIII	FWIII	FDIV	FWIV	TL	SHL	FOL	TFOL	TDI	TWI	TDII	TWII	TDIII	TWIII	TDIV	TWIV	TDV	TWV	IMT	OMT
CIB 65706	RS	male	0.4	0.4	0.4	0.4	9.7	10.1	9.9	14.3	0.4	0.4	0.4	0.4	0.4	0.4	0.5	0.5	0.4	0.4	0.9	0.7
CIB 65696	RS	male	0.4	0.4	0.4	0.4	9.8	10.4	9.7	14.0	0.4	0.4	0.4	0.4	0.5	0.5	0.5	0.5	0.4	0.4	1.0	0.7
CIB 65692	RS	male	0.4	0.4	0.4	0.4	8.0	9.8	9.6	14.0	0.4	0.4	0.4	0.4	0.4	0.4	0.5	0.5	0.4	0.4	0.8	0.7
CIB 65701	RS	male	0.5	0.5	0.4	0.4	8.6	10.0	9.4	14.0	0.4	0.4	0.5	0.5	0.5	0.5	0.5	0.5	0.5.	0.5	0.9	0.5
CIB 65691	RS	male	0.4	0.4	0.4	0.4	9.5	10.2	9.5	14.0	0.4	0.4	0.4	0.4	0.5	0.5	0.5	0.5	0.4	0.4	1.0	0.6
		Mean	0.4	0.4	0.4	0.4	9.2	10.2	9.7	14.1	0.4	0.4	0.4	0.4	0.5	0.5	0.5	0.5	0.4	0.4	0.9	0.6
		SD	0.0	0.0	0.0	0.0	0.7	0.3	0.2	0.1	0.0	0.0	0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.1	0.1	0.1
									Micri	Microhyla orientalis	entalis											
Vocuher No	status		SVL	ΜH	ΗΓ	SL	EL	EN	SS	IUE	UEW	Z	FAL	HAL	FIL	FIIL	FIIIL	FIVL	FDI	FWI	FDII	FWII
UIMZ 0037	RS	male	17.1	4.9	4.3	2.4	1.4	1.1	0.9	1.7	1.0	1.3	2.7	4.1	0.6	1.1	2.4	1.5	0.3	0.3	0.4	0.3

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0.5	0.5	0.5	0.4	0.4	0.1	OMT	0.6	0.8	0.8	0.8	0.9	0.8	0.1
0.5	0.5	0.5	0.4	0.4	0.1	IMT	0.8	0.6	0.7	0.7	0.7	0.7	0.1
0.4	0.4	0.4	0.4	0.4	0.0	TWV	0.4	0.5	0.4	0.5	0.5	0.5	0.1
0.4	0.4	0.4	0.4	0.4	0.0	TDV	0.4	0.5	0.4	0.5	0.5	0.5	0.1
1.6	1.7	1.6	1.5	1.6	0.1	TWIV	0.4	0.5	0.5	0.6	0.6	0.5	0.1
3.1	3.1	3.2	3.2	3.1	0.1	TDIV	0.4	0.5	0.5	0.6	0.6	0.5	0.1
1.4	1.6	1.7	1.6	1.6	0.1	TWIII	0.4	0.5	0.5	0.6	0.6	0.5	0.1
0.9	0.9	0.9	0.9	0.9	0.0	TDIII	0.4	0.5	0.5	0.6	0.6	0.5	0.1
5.0	5.1	5.1	5.0	5.0	0.1	IIWI	0.4	0.5	0.4	0.5	0.5	0.5	0.1
3.6	3.3	3.4	3.2	3.4	0.2	TDII	0.4	0.5	0.4	0.5	0.5	0.5	0.1
1.5	1.6	1.5	1.4	1.5	0.1	IWI	0.4	0.4	0.3	0.4	0.4	0.4	0.0
1.3	1.4	1.2	1.2	1.3	0.1	TDI	0.4	0.4	0.3	0.4	0.4	0.4	0.0
2.1	2.2	2.1	2.0	2.0	0.2	TFOL	14.5	14.3	14.3	14.6	13.8	14.3	0.3
0.9	0.9	1.0	0.9	0.9	0.1	FOL	11.5	10.7	10.3	10.7	10.2	10.7	0.5
1.5	1.4	1.4	1.4	1.4	0.1	SHL	11.3	10.3	10.1	10.3	10.0	10.4	0.5
1.9	1.8	1.6	1.5	1.7	0.2	ΤL	8.2	8.9	8.8	8.9	8.7	8.7	0.3
3.0	2.6	2.9	2.6	2.7	0.2	FWIV	0.3	0.4	0.4	0.5	0.4	0.4	0.1
5.7	5.6	5.1	5.2	5.4	0.3	FDIV	0.3	0.4	0.4	0.5	0.4	0.4	0.1
6.7	6.5	6.2	6.2	6.3	0.3	FWIII	0.4	0.5	0.5	0.5	0.4	0.5	0.1
22.7	22.0	22.3	21.3	21.9	0.7	FDIII	0.4	0.5	0.5	0.5	0.4	0.5	0.1
male	male	male	male	Mean	SD	sex	male	male	male	male	male	Mean	SD
RS	RS	RS	RS			status	RS	RS	RS	RS	RS		
CIB 67519	CIB 67540	CIB 67525	CIB 67535			Vocuher No	CIB 68500	CIB 67519	CIB 67540	CIB 67525	CIB 67535		

# ZooBank registration

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