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Four in one: An integrative taxonomic revision of the *Microhyla berdmorei* complex (Amphibia: Anura: Microhylidae) illustrates the tremendous amphibian diversity of Southeast Asia

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Abstract

Berdmore's narrow-mouthed frog, *Microhyla berdmorei* (Blyth, 1856), is the largest member of the genus *Microhyla* and is distributed all over Southeast Asia, from Northeast India and southern China to Sumatra and Borneo in Indonesia. Here we demonstrate that *M. berdmorei* represents a complex of four species that are morphologically, acoustically, and genetically distinct from each other, and we implement taxonomic revisions. Phylogenetic analyses of three mitochondrial DNA (hereafter mtDNA, including COI, 12S, and 16S rRNA; 3119 bp) and one nuclear (BDNF; 716 bp) gene sequences are corroborated by phylogenomic analyses of 2700 ddRAD-seq loci (387,270 bp). All support that the *M. berdmorei* complex, which originates from the early Miocene (ca. 19.7 mya), consists of two clades that we date to the late Miocene (ca. 7.5 mya). The first clade, which regroups populations of large-sized individuals, is distributed in Indo-Burma and includes a lineage from Northeast India, Bangladesh, and Myanmar (*M. berdmorei* sensu stricto) and a lineage from West Malaysia, Thailand, Laos, Cambodia, and Vietnam (for which we propose to resurrect the species *M. malcolmi* Cochran, 1927). The second clade, which regroups populations of small-sized individuals, occurs in Sundaland and also includes two lineages for which we provide taxonomic descriptions on species rank. The first new species is widely distributed

from Peninsular Malaysia to the islands of Borneo and Sumatra (described herein as *M. sundaica* **sp. nov.**), while the second one is restricted to the Malay Peninsula and occurs in extreme southern Thailand and adjacent Malaysia (*M. peninsularis* **sp. nov.**). We further provide evidence for the synonymy of *Callula natatrix* Cope, 1867 with *M. berdmorei* sensu stricto, and *M. fowleri* Taylor, 1934 with *M. malcolmi*. Our study illustrates the high diversity of Southeast Asian amphibians, especially in the genus *Microhyla*, which presently totals 54 species.

Keywords

Advertisement call, biodiversity, ddRAD-seq, Indochina, molecular phylogeny, morphology, mtDNA, narrow-mouthed frogs, new species, Sundaland

Introduction

The narrow-mouthed frogs, or *Microhyla* Tschudi, 1838, represent the most species-rich genus of the subfamily Microhylinae and are widely distributed from India, Pakistan, and Sri Lanka in the west to the Ryukyu Islands of Japan in the east, and southwards to the Indonesian Islands west of the Wallace Line (Gorin et al. 2020, 2021). Gorin et al. (2020) analyzed the phylogenetic relationships and historical biogeography of *Microhyla* and recognized eight species groups within this genus, namely *Microhyla achatina*, *M. fissipes*, *M. berdmorei*, *M. superciliaris*, *M. ornata*, *M. butleri*, *M. palmipes*, and *M. annectens* species groups, with the latter being subsequently transferred to the newly established genus *Nanohyla* (Gorin et al. 2021). Currently, *Microhyla* includes 51 nominal species, with over half of this diversity (31 species) having been described within the last 15 years (see Frost 2024). This surge of species descriptions can be partly explained by a wider application of the integrative taxonomic approach, in which detailed morphological, molecular, and bio-acoustic analyses led to the discovery of numerous previously unnoticed lineages worthy of taxonomic attention. For instance, new species have been described almost every year among the different *Microhyla* species complexes, such as in the *M. achatina* complex (Eprilurahman et al. 2021), the *M. butleri* complex (Nguyen et al. 2019; Poyarkov et al. 2020a), the *M. heymonsi* complex (Poyarkov et al. 2020b; Hoang et al. 2021, 2022; Garg et al. 2022; Eprilurahman et al. 2023), the *M. fissipes* complex (Li et al. 2019; Matsui and Tominaga 2020; Zhang et al. 2022), and the *M. superciliaris* complex (Biju et al. 2019; Garg et al. 2019; Poyarkov et al. 2020c). Most species of *Microhyla* have limited distributions, except for a few taxa with extensive ranges that encompass almost the entire Indo-Burma Region. The systematic and phylogeography of wide-ranged *Microhyla* species complexes yet remains insufficiently studied, and these may hide more candidate taxa than currently appreciated. However, available research is essentially based on mtDNA genetic markers, which are often insufficient to draw taxonomic conclusions (Dufresnes and Jablonski, 2022).

Berdmore's narrow-mouthed frog, *M. berdmorei* (Blyth, 1856), is the largest species of the genus, with adult females reaching up to 46 mm (Poyarkov et al.

2014); together with the other large-sized species *M. pulchra* (Hallowell, 1861), *M. picta* Schenkel, 1901 and *M. darevskii* Poyarkov et al., 2014, these taxa form the *M. berdmorei* species group (Gorin et al. 2020). As currently understood, *M. berdmorei* is widely distributed throughout Bangladesh, India, China, Myanmar, Laos, Cambodia, Vietnam, Thailand, Malaysia, and Indonesia (Poyarkov et al. 2014, 2021; Frost 2024). However, the differentiation of *M. berdmorei* populations across this extensive geographic range has not been comprehensively studied. *Microhyla berdmorei* was originally described from "Pegu, Burma" (now Bago Region, Myanmar) under the name *Engystoma berdmorei* by Blyth (1856). Currently, three taxa are regarded as subjective junior synonyms of *M. berdmorei* (see Frost 2024): *Callula natatrix* Cope, 1867 (type locality: near Yangon Region, Myanmar); *M. malcolmi* Cochran, 1927 (type locality: Pak Chong, Nakhon Ratchasima Province, Thailand); and *M. fowleri* Taylor, 1934 (type locality: Chiang Mai Province, Thailand). However, the status of *M. berdmorei* and its synonyms still remains controversial, largely due to a significant number of misidentifications that were made in the past (e.g., see note in Garg et al. 2019: 15). The taxonomic history of the *M. berdmorei* complex is summarized in Table 1. The validity of *M. fowleri* was first doubted based on its morphological similarity to *M. berdmorei* (see Bourret 1942; Taylor 1962) and Matsui et al. (2011), based on mtDNA sequences of topotypic specimens from Thailand, also suggested that these two taxa might be conspecific. However, *M. fowleri* is still recognized as a valid species by some authors (e.g., Yang and Rao 2008; Fei et al. 2009, 2010, 2012; Poyarkov et al. 2014; Li et al. 2019). In fact, the seminal work by Matsui et al. (2011), which represents the first molecular assessment of the subfamily Microhylinae, reported significant molecular divergence between populations of *M. berdmorei* in Malaysia and Indonesia and populations assigned to "*M. fowleri*" in Thailand. Subsequent studies provided further evidence for the existence of high genetic diversity and candidate taxa within the *M. berdmorei* complex (see Garg et al. 2019; Nguyen et al. 2019; Gorin et al. 2020; Kundu et al. 2021). However, a comprehensive, geographically-explicit analysis of the morphologi-

Table 1. Species-level scientific names erected for the members of the *Microhyla berdmorei* complex and the proposed taxonomic status.

No.	Authority	Original taxon name	Type locality	Previous taxonomy*	Proposed taxonomy
1	Blyth (1856 [“1855”])	<i>Engystoma</i> (?) <i>berdmorei</i>	Bago, Myanmar	<i>Microhyla berdmorei</i>	<i>Microhyla berdmorei</i>
2	Cope (1867)	<i>Callula natatrix</i>	near Yangon, Myanmar	Subjective junior synonym of <i>Microhyla berdmorei</i>	Subjective junior synonym of <i>Microhyla berdmorei</i>
3	Cochran (1927)	<i>Microhyla malcolmi</i>	Pak Chong, Nakhon Ratchasima, Thailand	Subjective junior synonym of <i>Microhyla berdmorei</i>	<i>Microhyla malcolmi</i>
4	Taylor (1934)	<i>Microhyla fowleri</i>	Chiang Mai, Thailand	Subjective junior synonym of <i>Microhyla berdmorei</i>	Subjective junior synonym of <i>Microhyla malcolmi</i>
5	This study	<i>Microhyla peninsularis</i>	Lam Plok Waterfall, Trang, Thailand	–	<i>Microhyla peninsularis</i> sp. nov.
6	This study	<i>Microhyla sundaica</i>	Sungai Tua, Selangor, Malaysia	–	<i>Microhyla sundaica</i> sp. nov.

* Previous taxonomy is given following Frost (2024).

cal and molecular variation of the *M. berdmorei* complex across its entire range, from which to implement robust taxonomic revisions, is presently lacking.

In this study, we use multilocus molecular, bioacoustic and morphological data to investigate the diversity and taxonomy of the *M. berdmorei* species complex, based on an extensive sampling from all over its range. Our analyses partially confirm and extend previous molecular studies (Garg et al. 2019; Gorin et al. 2020; Kundu et al. 2021) to populations that have never been examined. Our results support a hypothesis of four genetically and morphologically distinct species within the *M. berdmorei* species complex, of which two represent species new to science, described below.

Material and Methods

Species delimitation

In the lack of direct evidence for reproductive barriers, as revealed by absent or limited gene flow across secondary contact zones, species are herein delimited as sets of populations that belong to deeply-diverged, robustly supported lineages, eventually accompanied by external differences (“species lineages”, sensu Hillis 2019; Dufresnes et al. 2023; Vences et al. 2024). This approach has the advantage of combining the principles taken from the general lineage concept (GLC: de Queiroz 2007), in which a species constitutes a population of organisms evolving independently from other populations owing to a lack of gene flow (and thus represents an evolutionarily-independent lineage), with the biological species concept, where the lack of gene flow and genetic divergence reflects efficient reproductive isolation). To this end, mitochondrial data was used to identify candidate species lineages, i.e., monophyletic groups of individuals—the grouping stage of Hillis (2019) – that are further supported by the analyses of genome-wide nuclear data. Morphological data

were then used to search for unique characters and patterns consistent with these hypotheses—the construction of boundaries representing the hypothesis-testing step of Hillis (2019)—thus providing independent diagnoses in complement to molecular criteria.

Sample collection

A total of 85 ethanol-preserved specimens from the *M. berdmorei* complex were sampled for genetic analyses (Table S1). Specimens and tissues originated from the herpetological collections of the Zoological Museum of Moscow University (ZMMU, Moscow, Russia), the School of Agriculture and Natural Resources, the University of Phayao (AUP, Phayao, Thailand), the Joint Vietnam - Russia Tropical Science and Technology Research Center (VRTC/PVY, Hanoi, Vietnam), the Institute for Amphibian Biology, Hiroshima University (IABHU, Higashihiroshima, Japan), and the Departmental Museum of Zoology, Mizoram University (MZMU, Mizoram, India). The location of the examined populations and the distribution of the *M. berdmorei* species complex are shown in Figure 1. DNA was subsequently isolated from the thigh muscles or liver of vouchered specimens. Morphometric data were taken for 44 males and 32 females (the data summarized in Table 2 and Table S2).

For the purposes of this study, we additionally collected a series of *M. berdmorei* specimens from Vietnam and Thailand during our fieldwork in 2009–2022. Specimens were collected by hand during excursions along forest trails or in proximity to breeding sites, including temporary rain pools, rice fields, and swamps. Geographic coordinates and altitude data were accurately captured using a Garmin GPSMAP 60CSx GPS receiver and recorded in the WGS 84 datum. The specimens were euthanized using a 20% benzocaine solution. Prior to preservation, tissue samples were extracted for genetic analysis and stored in 96% ethanol; these samples included either femoral muscles or a piece of liver. Specimens were fixed in 10% buffered formalin and later transferred to 70%

Table 2 – Part A. Measurements (in mm) of the type series of *Microhyla sundaica* sp. nov. and *M. peninsularis* sp. nov.

No.	Species	Museum ID	Sex	Status	Location	SVL	HL	HW	SL	EL	N-EL	IND	IOD	UEW
1	<i>M. peninsularis</i> sp. nov.	ZMMU A-8017	M	Para-type	Thailand, Trang, Namtok Khao Chong	22.1	7.1	8.9	3.2	2.2	1.8	2.1	2.6	1.8
2	<i>M. peninsularis</i> sp. nov.	ZMMU A-8018	M	Para-type	Thailand, Trang, Namtok Khao Chong	22.2	6.9	7.6	3.2	2.5	1.8	2.0	2.5	1.3
3	<i>M. peninsularis</i> sp. nov.	ZMMU A-8015	F	Para-type	Thailand, Trang, Lam Plok Wf.	33.2	9.9	10.6	4.6	2.8	2.6	2.5	2.8	1.7
4	<i>M. peninsularis</i> sp. nov.	ZMMU A-8016	F	Holo-type	Thailand, Trang, Lam Plok Wf.	30.9	9.0	11.1	3.9	3.8	2.1	2.7	2.8	2.4
5	<i>M. sundaica</i> sp. nov.	ZMMU A-6158	M	Para-type	Malaysia, Pahang, Kuala Tahan	27.8	11.4	10.8	3.9	3.0	2.2	2.2	3.1	1.9
6	<i>M. sundaica</i> sp. nov.	ZMMU A-8014	M	Para-type	Malaysia, Selangor, Sungai Tua	27.9	9.0	10.4	3.8	2.8	2.1	2.6	2.7	1.9
7	<i>M. sundaica</i> sp. nov.	ZMMU A-8012	M	Para-type	Malaysia, Selangor, Sungai Tua	27.5	8.9	11.3	3.7	2.5	2.0	2.4	2.9	2.2
8	<i>M. sundaica</i> sp. nov.	ZMMU A-8010	F	Para-type	Malaysia, Selangor, Sungai Tua	28.4	9.4	10.2	3.9	2.8	1.9	2.3	3.2	2.0
9	<i>M. sundaica</i> sp. nov.	ZMMU A-8011	F	Holo-type	Malaysia, Selangor, Sungai Tua	31.4	9.6	11.2	4.3	3.2	2.2	2.6	3.3	2.2
10	<i>M. sundaica</i> sp. nov.	ZMMU A-8013	F	Para-type	Malaysia, Selangor, Sungai Tua	28.3	9.9	10.6	4.1	3.0	2.4	2.8	3.0	1.8

Table 2 – Part B. Measurements (in mm) of the type series of *Microhyla sundaica* sp. nov. and *M. peninsularis* sp. nov.

No.	Species	Museum ID	Sex	FLL	LAL	HAL	1FL	IPTL	OPTL	3FDD	HLL	TL	FL	IMTL	ITOEL	OMTL	4TDD
1	<i>M. peninsularis</i> sp. nov.	ZMMU A-8017	M	12.3	10.1	5.5	1.5	0.5	1.0	0.7	45.2	16.9	13.7	0.9	2.7	1.0	1.3
2	<i>M. peninsularis</i> sp. nov.	ZMMU A-8018	M	11.1	10.1	5.5	1.8	0.7	1.1	0.7	49.3	17.7	14.3	1.3	2.6	0.8	1.4
3	<i>M. peninsularis</i> sp. nov.	ZMMU A-8015	F	15.9	13.5	7.4	2.2	0.7	1.1	0.9	68.0	25.7	18.7	0.9	4.1	0.8	2.0
4	<i>M. peninsularis</i> sp. nov.	ZMMU A-8016	F	15.6	12.3	7.1	2.1	1.1	1.3	1.0	65.6	23.4	17.5	1.0	3.1	1.9	2.0
5	<i>M. sundaica</i> sp. nov.	ZMMU A-6158	M	16.0	12.6	5.4	1.8	1.1	1.1	0.7	58.7	21.5	15.9	1.0	3.8	1.0	1.7
6	<i>M. sundaica</i> sp. nov.	ZMMU A-8014	M	14.4	11.8	7.3	2.2	1.0	1.4	0.8	56.3	21.4	16.6	1.7	3.6	1.6	1.7
7	<i>M. sundaica</i> sp. nov.	ZMMU A-8012	M	14.8	12.3	6.9	2.3	1.0	1.4	1.1	58.4	21.0	16.4	1.6	3.6	1.6	1.7
8	<i>M. sundaica</i> sp. nov.	ZMMU A-8010	F	14.5	12.2	7.2	2.2	1.1	1.3	1.0	60.6	22.9	17.8	1.5	3.8	1.6	1.0
9	<i>M. sundaica</i> sp. nov.	ZMMU A-8011	F	16.8	13.9	7.9	2.8	1.0	1.4	1.1	66.4	23.6	19.5	1.4	4.6	2.0	1.9
10	<i>M. sundaica</i> sp. nov.	ZMMU A-8013	F	15.2	12.6	7.4	1.8	0.8	1.0	1.1	57.1	21.2	16.8	1.3	3.7	2.0	1.7

ethanol. Permissions to conduct fieldwork and collect specimens were granted by the Department of Forestry, Ministry of Agriculture and Rural Development of Vietnam (permit numbers #547/TCLN-BTTN; #432/TCLN-

BTTN; #822/TCLN-BTTN; #142/SNgV-VP; #1539/TCLN-DDPH; #1700/UBND.VX); the Forest Protection Departments of the Peoples' Committees of Gia Lai Province (permit numbers #530/UBND-NC; #1951/

Table 3. Comparison of morphological characteristics of the *Microhyla berdmorei* complex members (in mm).

Sex	Number	SVL	HL	SL	EL	N-EL	HW	IND	IOD	UEW	FLL	LAL	HAL	IFL
<i>Microhyla berdmorei sensu stricto</i>														
Adult male	N = 1	33.0	9.8	4.5	2.9	2.4	13.1	2.8	3.3	2.2	18.3	15.7	8.6	3.0
Adult females	N = 3	36.3±1.0	11.1±0.8	5.0±0.2	3.6±0.2	2.4±0.3	14.0±1.5	2.9±0.3	3.3±0.2	2.4±0.2	20.1±1.5	16.5±0.4	9.1±0.4	2.6±0.3
		36.3–38.1	10.6–11.9	4.8–5.3	3.5–3.8	2.1–2.6	12.8–15.7	2.7–3.2	3.1–3.6	2.2–2.5	19.2–21.8	16.2–16.9	8.7–9.5	2.3–2.9
<i>Microhyla malcolmi</i>														
Adult males	N = 22	36.3±2.4	14.3±1.2	4.9±0.4	3.9±0.3	2.7±0.5	14.3±1.5	2.4±0.3	3.5±0.3	2.4±0.3	20.2±1.7	15.8±1.2	7.7±1.4	2.6±0.4
		33.2–41.8	12.4–15.7	4.1–5.8	3.5–4.8	2.1–4.4	10.0–16.9	1.8–2.9	3.1–4.1	1.9–3.0	17.5–23.4	13.3–18.1	5.2–10.2	2.0–3.3
Adult females	N = 14	39.6±2.3	14.5±1.7	5.4±0.3	3.9±0.3	2.9±0.4	14.3±1.3	2.8±0.3	3.7±0.2	2.6±0.3	21.5±2.4	16.5±1.1	8.9±1.5	2.8±0.4
		36.0–43.8	11.1–16.8	4.8–5.9	3.2–4.3	2.1–3.6	11.8–16.7	2.2–3.3	3.4–4.0	1.9–2.9	18.0–25.4	15.0–18.5	6.4–11.5	2.0–3.4
<i>Microhyla peninsularis sp. nov.</i>														
Adult males	N = 2	22.1±0.1	7.0±0.1	3.2±0.0	2.3±0.2	1.8±0.0	8.2±0.9	2.1±0.1	2.5±0.1	1.5±0.3	11.7±0.9	10.1±0.0	5.5±0.0	1.6±0.2
		22.1–22.2	7.0–7.1	3.2–3.2	2.2–2.5	1.8–1.8	7.6–8.9	2.0–2.1	2.5–2.6	1.3–1.8	11.1–12.3	10.1–10.1	5.5–5.5	1.5–1.8
Adult females	N = 2	32.1±1.6	9.5±0.6	4.3±0.5	3.3±0.7	2.3±0.3	10.9±0.4	2.6±0.1	2.8±0.0	2.1±0.5	15.7±0.2	12.9±0.2	7.3±0.2	2.2±0.1
		30.9–33.2	9.1–9.9	3.9–4.6	2.8–3.8	2.1–2.6	10.6–11.1	2.5–2.7	2.8–2.8	1.7–2.4	15.6–15.9	12.3–13.5	7.1–7.4	2.1–2.2
<i>Microhyla sundatca sp. nov.</i>														
Adult males	N = 3	27.7±0.2	9.8±1.4	3.8±0.1	2.8±0.3	2.1±0.1	10.8±0.5	2.4±0.2	2.9±0.2	2.0±0.2	15.1±0.8	12.2±0.4	6.5±1.0	2.1±0.3
		27.5–27.9	8.9–11.4	3.7–3.9	2.5–3.0	2.0–2.2	10.4–11.3	2.2–2.6	2.7–3.1	1.9–2.2	14.4–16.0	11.8–12.6	5.4–7.3	1.8–2.3
Adult females	N = 3	29.4±1.8	9.6±0.3	4.1±0.2	3±0.2	2.2±0.3	10.7±0.5	2.6±0.3	3.2±0.2	2±0.2	15.5±1.2	12.9±0.9	7.5±0.4	2.3±0.5
		28.3–31.4	9.4–9.9	3.9–4.3	2.8–3.2	1.9–2.4	10.2–11.2	2.3–2.8	3.0–3.3	1.8–2.2	14.5–16.8	12.2–13.9	7.2–7.9	1.8–2.8
<i>Microhyla berdmorei sensu stricto</i>														
Adult male	N = 1	33.0	9.8	4.5	2.9	2.4	13.1	2.8	3.3	2.2	18.3	15.7	8.6	3.0
Adult females	N = 3	36.3±1.0	11.1±0.8	5.0±0.2	3.6±0.2	2.4±0.3	14.0±1.5	2.9±0.3	3.3±0.2	2.4±0.2	20.1±1.5	16.5±0.4	9.1±0.4	2.6±0.3
		36.3–38.1	10.6–11.9	4.8–5.3	3.5–3.8	2.1–2.6	12.8–15.7	2.7–3.2	3.1–3.6	2.2–2.5	19.2–21.8	16.2–16.9	8.7–9.5	2.3–2.9
<i>Microhyla malcolmi</i>														
Adult males	N = 22	36.3±2.4	14.3±1.2	4.9±0.4	3.9±0.3	2.7±0.5	14.3±1.5	2.4±0.3	3.5±0.3	2.4±0.3	20.2±1.7	15.8±1.2	7.7±1.4	2.6±0.4
		33.2–41.8	12.4–15.7	4.1–5.8	3.5–4.8	2.1–4.4	10.0–16.9	1.8–2.9	3.1–4.1	1.9–3.0	17.5–23.4	13.3–18.1	5.2–10.2	2.0–3.3
Adult females	N = 14	39.6±2.3	14.5±1.7	5.4±0.3	3.9±0.3	2.9±0.4	14.3±1.3	2.8±0.3	3.7±0.2	2.6±0.3	21.5±2.4	16.5±1.1	8.9±1.5	2.8±0.4
		36.0–43.8	11.1–16.8	4.8–5.9	3.2–4.3	2.1–3.6	11.8–16.7	2.2–3.3	3.4–4.0	1.9–2.9	18.0–25.4	15.0–18.5	6.4–11.5	2.0–3.4
<i>Microhyla peninsularis sp. nov.</i>														
Adult males	N = 2	22.1±0.1	7.0±0.1	3.2±0.0	2.3±0.2	1.8±0.0	8.2±0.9	2.1±0.1	2.5±0.1	1.5±0.3	11.7±0.9	10.1±0.0	5.5±0.0	1.6±0.2
		22.1–22.2	7.0–7.1	3.2–3.2	2.2–2.5	1.8–1.8	7.6–8.9	2.0–2.1	2.5–2.6	1.3–1.8	11.1–12.3	10.1–10.1	5.5–5.5	1.5–1.8
Adult females	N = 2	32.1±1.6	9.5±0.6	4.3±0.5	3.3±0.7	2.3±0.3	10.9±0.4	2.6±0.1	2.8±0.0	2.1±0.5	15.7±0.2	12.9±0.9	7.3±0.2	2.2±0.1
		30.9–33.2	9.1–9.9	3.9–4.6	2.8–3.8	2.1–2.6	10.6–11.1	2.5–2.7	2.8–2.8	1.7–2.4	15.6–15.9	12.3–13.5	7.1–7.4	2.1–2.2
<i>Microhyla sundatca sp. nov.</i>														
Adult males	N = 3	27.7±0.2	9.8±1.4	3.8±0.1	2.8±0.3	2.1±0.1	10.8±0.5	2.4±0.2	2.9±0.2	2.0±0.2	15.1±0.8	12.2±0.4	6.5±1.0	2.1±0.3
		27.5–27.9	8.9–11.4	3.7–3.9	2.5–3.0	2.0–2.2	10.4–11.3	2.2–2.6	2.7–3.1	1.9–2.2	14.4–16.0	11.8–12.6	5.4–7.3	1.8–2.3
Adult females	N = 3	29.4±1.8	9.6±0.3	4.1±0.2	3±0.2	2.2±0.3	10.7±0.5	2.6±0.3	3.2±0.2	2±0.2	15.5±1.2	12.9±0.9	7.5±0.4	2.3±0.5
		28.3–31.4	9.4–9.9	3.9–4.3	2.8–3.2	1.9–2.4	10.2–11.2	2.3–2.8	3.0–3.3	1.8–2.2	14.5–16.8	12.2–13.9	7.2–7.9	1.8–2.8

UBND-NV), Phu Yen Province (permit number #05/UBND-KT); Phu Tho Province (permit number #2394/UBND-TH3); Thanh Hoa Province (permit number #3532/UBND-THKH); and Quang Nam Province (permit number #308/SNgV-LS), Vietnam; by the Department of Forestry, Ministry of Agriculture and Forestry of Lao PDR (permit number #271/08, form #511); by the Forestry Department of Peninsular Malaysia (permit number #KT 01-16/2015); by the Chief Wildlife Warden, Department of Environment, Forest and Climate Change, Government of Mizoram, India (permit number No.A.33011/2/99-CL-WL/225); and by the Institute of Animals for Scientific Purpose Development (IAD), Bangkok, Thailand (permit number U1-01205-2558). Specimen collection protocols and animal operations followed the Institutional Ethical Committee of Animal Experimentation of the University of Phayao, Phayao, Thailand (certificate number UP-AE61-01-04-0022).

Overall, we examined morphological, genetic and photographic data from the material deposited in the following herpetological collections: **ANSP**: Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania, USA; **AUP**: School of Agriculture and Natural Resources, University of Phayao, Phayao, Thailand; **CAS**: California Academy of Sciences Museum, San Francisco, California, USA; **DFBSFMSTU**: Department of Fisheries, Bangamata Sheikh Fazilatunnesa Mujib Science & Technology University, Jamalpur, Bangladesh; **FRIM**: Forest Research Institute Malaysia, Kuala Lumpur, Malaysia; **IABHU**: Institute for Amphibian Biology, Hiroshima University, Hiroshima, Japan; **ITB**: Institute of Tropical Biology, Ho Chi Minh, Vietnam; **KUHE**: Graduate School of Human and Environmental Studies, Kyoto University, Kyoto, Japan; **MCZ**: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; **MZB**: Museum Zoologicum Bogoriense, Java, Indonesia; **MZMU**: Museum of the Zoology Department, Mizoram University, Mizoram, India; **RMBR**: Danum Valley Conservation Area, Sabah, Malaysia; **SDBNU**: Systematics Lab, University of Delhi, Dehli, India; **UNIMAS**: Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak, Sarawak, Malaysia; **USNM**: National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; **VRTC**: Joint Vietnam – Russia Tropical Science and Technology Research Center, Hanoi, Vietnam; **WII**: Wildlife Institute of India, Uttarakhand, India; **ZISP**: Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia; **ZMMU**: Zoological Museum of Moscow State University, Moscow, Russia.

Morphological description and analyses

For this study, a total of 66 preserved specimens of the *M. berdmorei* species complex were examined for their external morphological characters (see Tables 2, 3, S2). We also examined photographs of the syntype (MCZ A-1587) of *Callula natatrix* Cope, the holotype (USNM

72172) of *M. malcolmi* Cochran, as well as the holotype (ANSP 19903) of *M. fowleri* Taylor. Measurements were taken using a Mitutoyo digital caliper to the nearest 0.01 mm and subsequently rounded to the nearest 0.1 mm. We used an Olympus stereoscopic light binocular microscope when necessary. All measurements were taken on the right side of the examined specimen.

The morphometrics of adults and character terminology followed Poyarkov et al. (2014, 2018a, 2019) and included the following measurements: (1) snout-vent length (**SVL**; distance from tip of snout to cloaca); (2) head length (**HL**; distance from tip of snout to the posterior border of jaw angle); (3) snout length (**SL**; distance from anterior corner of eye to tip of snout); (4) eye length (**EL**; distance between anterior and posterior corners of the eye); (5) nostril-eye length (**N-EL**; distance between anterior corner of eye and nostril center); (6) head width (**HW**; maximum width of the head at level of mouth angles in ventral view); (7) internarial distance (**IND**; distance between central points of nostrils); (8) interorbital distance (**IOD**; shortest distance between medial edges of eyeballs in dorsal view); (9) upper eyelid width (**UEW**; maximum distance between medial edge of eyeball and lateral edge of upper eyelid, in dorsal view); (10) forelimb length (**FLL**; length of straightened forelimb from axilla to tip of third finger); (11) lower arm and hand length (**LAL**; distance between elbow and tip of third finger); (12) hand length (**HAL**; distance between proximal end of outer palmar (metacarpal) tubercle and tip of third finger); (13) first finger length (**1FL**, distance between tip and distal end of inner palmar tubercle); (14) inner palmar tubercle length (**1PTL**; maximum distance between proximal and distal ends of inner palmar tubercle); (15) outer palmar tubercle length (**OPTL**; maximum diameter of outer palmar tubercle); (16) third finger disk diameter (**3FDD**); (17) hindlimb length (**HLL**; length of straightened hindlimb from groin to tip of fourth toe); (18) tibia length (**TL**; distance between knee and tibiotarsal articulation); (19) foot length (**FL**; distance between distal end of tibia and tip of fourth toe); (20) inner metatarsal tubercle length (**IMTL**; maximum length of inner metatarsal tubercle); (21) outer metatarsal tubercle length (**OMTL**); (22) first toe length (**1TOEL**), from distal end of inner metatarsal tubercle to tip of first toe; and (23) fourth toe disk diameter (**4TDD**). Toe webbing and subarticular tubercle formulas were described following Savage (1975). The sex and maturity of the specimens were checked by minor dissections and direct observation of calling in living males prior to collection. Other abbreviations: **Dist.**: District; **FR**: Forest Reserve; **Mt.**: Mountain; **NP**: National Park; **NR**: Natural Reserve; **Prov.**: Province. Among the examined populations, SVL was compared using a one-way ANOVA with the Tukey-Kramer test. The percentage ratio (R) of each morphometric character to SVL was subsequently calculated; we compared 22 character ratios against SVL among populations using the Kruskal-Wallis test. PCA was conducted to examine overall morphological variation among populations using log_e-transformed metric values following Nishikawa et al. (2007). When a high correlation between certain pairs

of characters was found, we omitted one of them from the analyses to exclude possible overweighting effects. Statistical analyses were performed with Statistica 6.0 (StatSoft Inc. 2001). The significance level was $P < 0.05$.

For comparison with other taxa of the *M. berdmorei* species group, we relied on previously published data (e.g., Blyth 1856; Hallowell 1861; Cope 1867; Schenkel 1901; Cochran 1927; Taylor 1934, 1962; Fei et al. 2009, 2010, 2012; Poyarkov et al. 2014).

Laboratory methods

For mtDNA and BDNF gene sequencing, we extracted total genomic DNA from ethanol-preserved femoral or liver muscle tissue using standard phenol-chloroform-proteinase K extraction with consequent isopropanol precipitation for a final concentration of ~1 mg/mL (protocols followed by Hillis et al. 1996; Russell and Sambrook 2001). For ddRAD-seq analysis, DNA was isolated using an ad hoc salt protocol (Bruford et al. 1992). We visualized the isolated total genomic DNA using agarose electrophoresis in the presence of ethidium bromide or midori green stain.

We amplified two mtDNA fragments, namely a fragment partially covering the 12S rRNA–16S rRNA genes and the complete sequence of tRNA-Val (up to 2474 bp) and a fragment covering the 5'-end of the COI mtDNA gene (up to 645 bp), totalling 3119 bp. These markers have proven to offer a sufficient resolution for species discovery and identification in the genus *Microhyla* (e.g., Matsui 2011; Hasan et al. 2012, 2014; Matsui et al. 2013; Wijayathilaka et al. 2016; Garg et al. 2019; Poyarkov et al. 2019, 2020b, 2020c; Gorin et al. 2020). DNA amplification was performed in 20- μ L reactions using ca. 50 ng genomic DNA, 10 nmol of each primer, 15 nmol of each dNTP, 50 nmol additional MgCl₂, Taq PCR buffer (10 mM Tris-HCl, pH 8.3, 50 mM KCl, 1.1 mM MgCl₂, and 0.01% gelatine), and 1 U of 185 Taq DNA polymerase. Additionally, for nuDNA species barcoding, we amplified a 716 bp-long fragment of the brain-derived neurotrophic factor gene (BDNF). This marker has accordingly been used in biodiversity and phylogenetic analyses of *Microhyla* (see Biju et al. 2019; Garg et al. 2019; Gorin et al. 2020).

Primers used in PCR and sequencing for the 12S rRNA–16S rRNA mtDNA fragment and the BDNF gene, along with the PCR conditions, followed Gorin et al. (2020). Primers used in PCR and sequencing and the PCR conditions for the COI mtDNA gene followed Che et al. (2012) and Vences et al. (2012). Primers used for DNA amplification and sequencing are summarized in Table S3. PCRs were run on a Bio-Rad T100TM Thermal Cycler. The PCR conditions for amplifying mtDNA fragments included an initial denaturation step of 5 min at 94°C, 40 cycles of denaturation for 1 min at 94°C, a primer annealing step for 1 min with the TouchDown program from 65°C reducing 1°C every cycle to 55°C, an extension step for 1 min at 72°C, and the final extension step for 5 min at 72°C. The PCR conditions for amplifying

the BDNF gene followed van der Meijden et al. (2007) and included an initial denaturation step of 5 min at 94°C followed by 32 cycles of denaturation for 1 min at 94°C, a primer annealing step for 1 min at 50°C, and an extension for 1 min at 72°C, with a final extension step for 5 min at 72°C.

The PCR products were loaded onto 1.5% agarose gels in the presence of ethidium bromide and visualized in electrophoresis. The successful targeted PCR products were outsourced to Evrogen® (Moscow, Russia) for PCR purification and bidirectional sequencing from both the forward and reverse primers. Sequence data collection and visualization were carried out on an ABI 3730xl Automated Sequencer (Applied Biosystems). We deposited the newly obtained sequences in GenBank under the accession numbers PP790531–PP790548, PP778115–PP778197, and PP795498–PP795544 (see Table S1 for details).

Phylogenetic analyses of mtDNA markers and the BDNF gene

The matrilineal genealogy of *Microhyla* was reconstructed using a concatenated dataset comprising 12S–16S rRNA and COI mtDNA sequences of *M. berdmorei* complex members obtained from GenBank and our newly acquired sequences. The final analysis incorporated data from 135 specimens, including a sequence of *Kaloula pulchra* Gray, 1831, which was used as outgroup to root the phylogenetic tree (see Table S1 for details). The DNA sequences were initially aligned using MAFFT v.6 (Katoh et al. 2002) with default parameters, followed by minor adjustments in BioEdit v.7.0.5.2 (Hall 1999). The average uncorrected genetic distances (p distances) between individuals were computed using MEGA 6.0 (Tamura et al. 2013). The IQ-TREE web server (Nguyen et al. 2015; Trifinopoulos et al. 2016) was employed to determine the optimal evolutionary models for subsequent analysis. The best-fit DNA evolution models are summarized in Table S4.

The matrilineal genealogy was inferred using both Maximum Likelihood (ML) and Bayesian Inference (BI) methodologies. The ML analysis was conducted on the IQ-TREE webserver. We employed 10000 bootstrap pseudoreplicates via the ultrafast bootstrap (hereafter ML UFBS; Hoang et al. 2018) approximation algorithm to infer confidence in tree nodes. Nodes with ML UFBS values of 95 and above were considered highly supported, while nodes with values ranging from 90 to 94 were regarded as well-supported (following Bui et al. 2013). The BI analysis was implemented in MrBayes v. 3.1.2 (Ronquist and Huelsenbeck 2003). Metropolis-coupled Markov chain Monte Carlo (MCMCMC) analyses were run with one cold and three heated chains over 20 million generations, with sampling conducted every 2000 generations. Two independent MCMCMC runs were performed, and the effective sample sizes (ESSs) were confirmed to be above 200 by examining the likelihood plots using TRACER v. 1.6 (Rambaut et al. 2014). The initial 1000

trees were discarded as burned-in. In BI analysis, the confidence in tree topology was assessed by the frequency of nodal resolution (posterior probability; hereafter BI PP) (Huelsenbeck and Ronquist 2001). Tree nodes with BI PP values over 0.95 were considered to be strongly supported; values between 0.95 and 0.90 were regarded as moderately supported, while values lower than 0.90 were considered to lack nodal support (Huelsenbeck and Hillis 1993). The allele network for the BDNF gene was constructed using the median-joining method in PopArt ver. 1.5 (Leigh and Bryant 2015) with a 95% connection limit.

ddRAD-seq analyses

To infer the nuclear differentiation of the candidate species identified by the mitochondrial analyses, we analyzed 16 *Microhyla* individuals (Table S1), including 12 from the *M. berdmorei* species complex (11 localities, representative of all candidate species lineages) and four from *M. pulchra* to be used as outgroups through double-digest Restriction Associated DNA sequencing (ddRAD-seq). To this end, the individuals were included in a genomic library prepared with a custom protocol (<http://dx.doi.org/10.17504/protocols.io.kxygx3nzwg8j/v1>), adapted from Brelford et al. (2016), and sequenced on an DNBSEQ-G400 with the PE150 kit. Single-end reads were demultiplexed with STACKS 2.63 (Catchen et al. 2013) and the `denovo_map.pl` pipeline was applied for RAD loci construction, assembly, and cataloguing (default `-m`, `-n`, and `-M` values). A supermatrix alignment (phylip format, including variable and invariable sites) was obtained with the module population of STACKS, by considering the loci sequenced in at least 12 of the 16 samples (`-p 12 -phylip-var-all`). The alignment was converted to fasta format using an online tool (https://www.hiv.lanl.gov/content/sequence/FORMAT_CONVERSION/form.html). A maximum-likelihood tree was then built with IQ-TREE 1.6 (Trifinopoulos et al. 2016), using the model finder tool to find and apply the best model of sequence evolution, and 1000 ultrafast bootstrap replicates to assess node support. Functions from various R packages (`ggtree`, `tidytree`, `dplyr`) were employed to visualize and edit the obtained phylogenomic tree. Raw demultiplexed RAD-sequencing reads were deposited on NCBI Sequence Read Archive (SRA) under BioProject PRJNA949685 (accession numbers SAMN44502878-SAMN44502893).

Divergence time estimation

We performed molecular divergence dating using BEAST v2.6.5 (Bouckaert et al. 2019). For the analysis, we used additional datasets from taxon-wise broader research on the *Microhyla-Nanohyla-Glyphoglossus* assemblage (Gorin et al. 2020, 2021, 2023), with *M. berdmorei* sampling cut to one lineage per clade and other species represented by one lineage each (Table S5). Calibration points and molecular clock assumptions followed Gorin et al. (2020), and included three secondary calibrations from

Kurabayashi et al. (2011), and three calibrations based on geological or fossil data (from Holman 2003, Fromhage et al. 2004, and Vences et al. 2003) (summarized in Table S6). Partitioning schemes followed those used in ML/BI analyses, with substitution models adjusted due to the limitations of BEAST software. We used the GTR+I+G model for the 12S–16S rRNA mtDNA fragment, TN93/HKY+G/GTR+G for 1/2/3 codon positions of the COI gene of mtDNA, respectively, and GTR+G/HKY/GTR+G for 1/2/3 codon positions of the BDNF gene of nuDNA, respectively. Chain length was set to 400 million generations, and trees were sampled every 40,000 generations, resulting in a set of 10,000 trees. We used Tracer v1.6 (Rambaut et al. 2014) to ensure that the effective sample sizes (ESS) were all above 200, with 10% of generations discarded as burn-in. Finally, we used TreeAnnotator v2.6.3 (from the BEAST 2 software package) to calculate the maximum clade credibility tree (MCC) with median node heights based on the set of trees obtained earlier.

Acoustic analysis

Advertisement calls of three populations of the *M. berdmorei* species complex were recorded using a portable digital audio recorder Zoom h5 (ZOOM Corporation, Tokyo, Japan) in stereo mode with 48 kHz sampling frequency and 16-bit precision. The records were taken in Song Hinh Forest Reserve, Phu Yen Province, Vietnam (locality 10, see Fig. 1; on 12 and 13 January 2021 at 22.45 h and at 17°C), in Aizawl, Mizoram State, India (locality 33, see Fig. 1; on 20 November 2022 at 21.00 h and at 23°C), and in Gunung Jerai Mt., Kedah, Peninsular Malaysia (on 30 January 2010 at 20.00 h and at 25°C). The ambient temperature was measured at the calling site immediately after the audio recording with a digital thermometer KJT TA218A Digital LCD Thermometer-Hydrometer. Males were observed calling from the banks of a small temporary water pools, while hiding under the leaves approximately in 5–10 cm from the waters' edge. When disturbed males stopped calling and hid in leaf litter. At each locality, calls from three individual males were recorded.

Calls were analyzed using Avisoft SASLab Pro software v.5.2.14 (Avisoft Bioacoustics, Germany). Before analysis, we reduced the background noise using a low-pass filter (up to 500 Hz). All temporal parameters were analyzed with the standard marker cursor in the main window of Avisoft and frequencies of the maximum amplitude of calls and pulses were measured in the power spectrum. The spectrogram for analysis was created using a Hamming window, with FFTlength 512 points, frame 75%, and overlap 93.75%. For graphic representation of spectrograms, we lowered the sampling rate to 22.05 kHz. Figures of spectrograms were created using a Hamming window, with FFT-length 512 points, frame 50%, and overlap 93.75%. In total, we measured 35 calls from three males of the *M. berdmorei* complex from three different localities.

Due to the poor quality of the recordings, we were able to measure six temporal parameters: i.e., number of calls

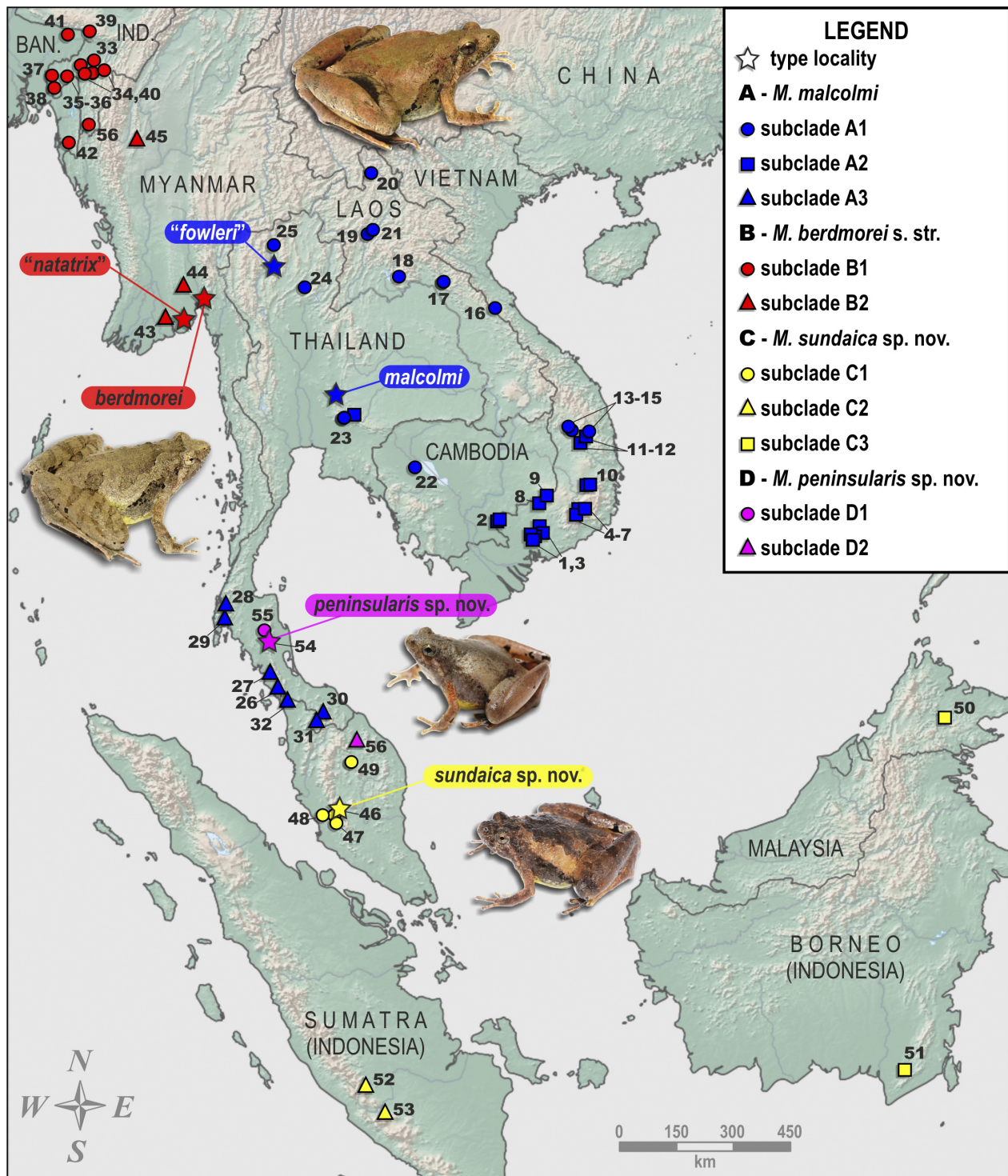


Figure 1. Distribution of the species lineages of the *Microhylya berdmorei* species complex as identified in the phylogenetic analyses. Star denotes type localities, with their corresponding taxon names in colored clouds; synonyms are shown in quotes; colors correspond to those used in Figures 2–5; symbol shapes denote mtDNA lineages shown in Figure 2. Base map created using simplemapp.net. For locality information see Table S1. Photos by A. V. Trofimets, A. M. Bragin, P. Pawangkhanant and N. A. Poyarkov.

per series, call duration, intervals between successive calls within series, number of pulses per call, duration of pulses, intervals between successive pulses; and two power parameters: i.e., frequency of maximum amplitude (F_{peak}) of calls and of pulses. Most numeral parameters are given as means \pm SE and the minimum and maximum values are given in parentheses (min–max).

Results

Characteristics of the genetic datasets

A total of 3119 bp (645 bp from COI and 2474 bp from the 12S rRNA–16S rRNA fragment, respectively) aligned

Table 4. Uncorrected p distances (percentage) between the sequences of 16S rRNA mtDNA gene of members of the *Microhyala berdmorei* complex.

Taxon	Clade	<i>M. malcolmi</i> (mOTU1)			<i>M. berdmorei</i> sensu stricto (mOTU2)		<i>M. sundaica</i> sp. nov. (mOTU3)			<i>M. peninsularis</i> sp. nov. (mOTU4)	
		A1	A2	A3	B1	B2	C1	C2	C3	D1	D2
<i>Microhyala malcolmi</i> (mOTU1)	A1	0.31%									
	A2	0.94%	0.76%								
	A3	0.92%	0.79%	0.07%							
<i>Microhyala berdmorei</i> sensu stricto (mOTU2)	B1	2.02%	1.98%	1.92%	0.09%						
	B2	1.77%	1.76%	1.77%	0.71%	0.08%					
<i>Microhyala sundaica</i> sp. nov. (mOTU3)	C1	2.22%	2.31%	1.49%	2.79%	2.89%	0.08%				
	C2	2.88%	2.92%	2.06%	3.29%	3.55%	0.81%	0.67%			
	C3	2.83%	2.86%	2.18%	3.03%	3.03%	1.59%	2.05%	0.62%		
<i>Microhyala peninsularis</i> sp. nov. (mOTU4)	D1	3.34%	3.35%	2.49%	3.79%	3.55%	1.90%	2.48%	2.16%	0.00%	
	D2	2.93%	2.91%	2.07%	2.95%	3.13%	1.49%	2.05%	2.16%	1.24%	n/c

were recovered: one corresponding to the *M. berdmorei* species complex and one regrouping *M. pulchra* and *M. picta*, though with a moderate level of support in ML analysis (95/1.0). The monophyly of the *M. berdmorei* complex was strongly supported (100/1.0); it included in total four mOTUs (molecular operational taxonomic units) arranged in two clades.

The first clade (98/1.0) is distributed in the mainland Indo-Burma Region and the northern part of the Thai-Malay Peninsula and includes two mOTUs (see Fig. 2B): mOTU1 (98/1.0), which comprises populations from the mainland Indochina, including southern Vietnam (localities 1–21, 23; subclade A1), central and northern Indochina (localities 13–25; subclade A2), and peninsular Thailand (localities 26–32; subclade A3). The range of mOTU1 includes the type localities of *M. malcolmi* Cochran, 1927, and *M. fowleri* Taylor, 1934 (Fig. 1).

mOTU2 (100/1.0) which comprises populations from the western Indo-Burma Region, including northeast India and Bangladesh (localities 32–42; subclade B1) and Myanmar (localities 43–45; subclade B2). The range of mOTU2 includes the type localities of *Engystoma berdmorei* Blyth, 1856, and *Callula natatrix* Cope, 1867 (Fig. 1).

The second clade (99/1.0) is distributed across the Sundaland, including the islands of Borneo, Sumatra, and Peninsular Malaysia; the ranges of two clades overlaps in southern Peninsular Thailand (see Fig. 1). This clade also includes two mOTUs (see Fig. 2B): mOTU3 (100/1.0), which comprises populations from Peninsular Malaysia (localities 46–49; subclade C1), Sumatra (localities 52–53; subclade C2), and Borneo (localities 50–51; subclade C3).

mOTU4 (100/1.0), which comprises populations from the Thai-Malay Peninsula, including Trang Province of Thailand (localities 54–55; subclade D1) and Terengganu State in Malaysia (locality 56; subclade D2).

In summary, the matrilineal genealogy reveals four mOTUs grouped in two clades within the *M. berdmorei*

species complex: one with distribution in the continental Indo-Burma Region and another in the Sundaland Region.

In the BDNF gene haplotype network, the *M. berdmorei* species complex is separated from its closest relatives, *M. pulchra* and *M. picta*, by at least eight mutational steps (Fig. 2A). Within the *M. berdmorei* complex, mOTU1 and mOTU2 share the same BDNF haplotype, while mOTU3 and mOTU4 each corresponds to a distinct BDNF haplotype, separated by at least one mutational step (Fig. 2A).

16S Genetic distances

The uncorrected p distances for the 16S rRNA mtDNA fragment among the members of the *M. berdmorei* species complex are summarized in Table 4. The interspecific distances among the members of the *M. berdmorei* complex varied from $p = 1.86\%$ (between mOTU1 and mOTU2; range 1.76%–2.02%) to $p = 3.51\%$ (between mOTU2 and mOTU4; range 2.95%–3.79%). Inter-group genetic differentiation among the subclades within the revealed mOTUs was small and varied from $p = 0.7\%$ (between the subclades B1 and B2 of mOTU2; range 0.0%–1.06%) to $p = 1.6\%$ (between the subclades C1 and C3 of mOTU3; range 1.22%–2.04%); therefore, the genetic distances for comparisons between mOTU and within mOTU slightly overlapped.

Phylogenomic analyses

The ddRAD-seq phylogenomics fully supported the mitochondrial analyses. Samples belonging to separate mOTUs from the *M. berdmorei* complex correspond to divergent nuclear lineages, which phylogenetic relationships matched the mtDNA tree topology. (Fig. 3). Namely, this includes two clades, each with two sets of samples: mOTU1 + mOTU2 and mOTU3 + mOTU4. Within the widespread mOTU1, the ddRADseq analysis also recov-

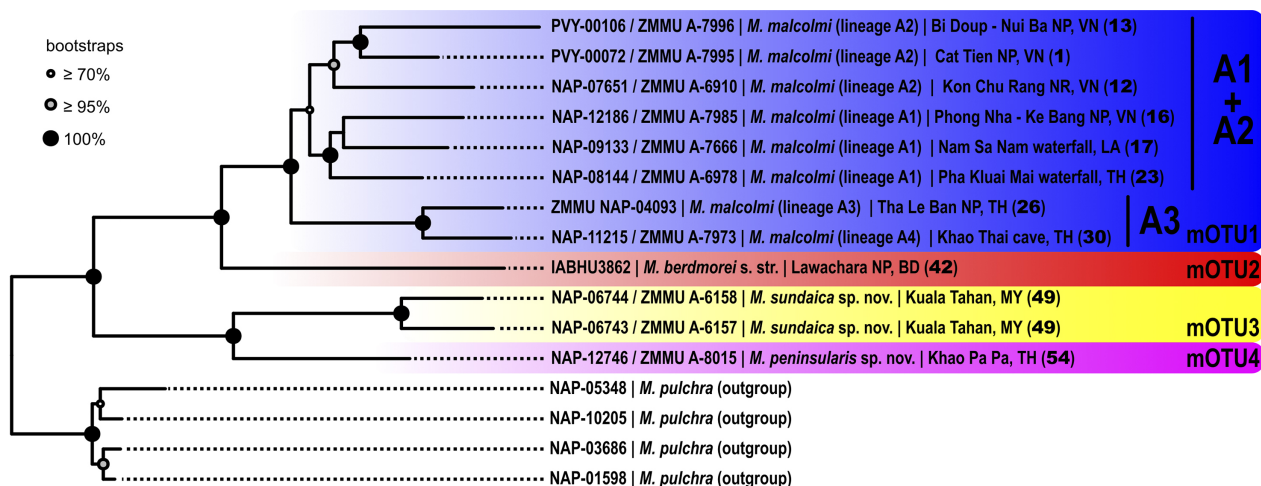


Figure 3. Phylogenetic relationship among the candidate species lineages of the *Microhyla berdmorei* species complex based on an ML analysis of 2700 ddRAD-seq loci (387,270 bp). Sequences of *M. pulchra* were used as outgroups. Colors correspond to those used in Figures 1–5; locality numbers given in brackets are presented in Figure 1 and detailed in Table S1.

ers the geographic structuring suspected from the mtDNA analyses: samples from southern Thailand, corresponding to the mtDNA subclade A3, formed a separate lineage, while samples bearing the mtDNA subclades A1 and A2 also form separate, although closely related and moderately supported lineages (Fig. 3).

Divergence time estimation

The calibrated phylogenetic analysis in BEAST provided a time tree that is presented in Figure S2. Since the topology and node age estimations are generally concordant with the results of Gorin et al. (2020, 2021), here we only report on age estimates relevant to the *M. berdmorei* species group. According to the present analyses, the most recent common ancestor (MRCA) of the *M. berdmorei* group is dated to the early Miocene, ca. 19.7 million years ago (mya) [12.0–27.5], while the split between *M. picta* and *M. pulchra* is estimated to have taken place ca. 15.4 mya. The diversification of the *M. berdmorei* species complex likely started in the late Miocene at ca. 7.5 mya [5.31–10.97]. The split between mOTU4 from the Thai-Malay Peninsula and mOTU3 from the Sundaland area was also dated to the Miocene-Pliocene transition, ca. 5.7 mya [3.6–9.1], shortly followed by the divergence between mOTU1 and mOTU2, ca. 5.2 mya [3.1–8.1]. Estimated node ages and the 95% highest posterior density (95% HPD) for the main nodes are presented in Figure S2; median age estimates for the key nodes are also summarized in Figure 2B.

Morphological differentiation

Among the mOTUs examined, the mean SVL varies substantially, ranging from 22.1 to 41.8 mm in males and from 28.3 to 43.8 mm in females (summarized in Tables 4, S2). Body size variation among adult males and females of *M. berdmorei* complex members is shown in figure 4.

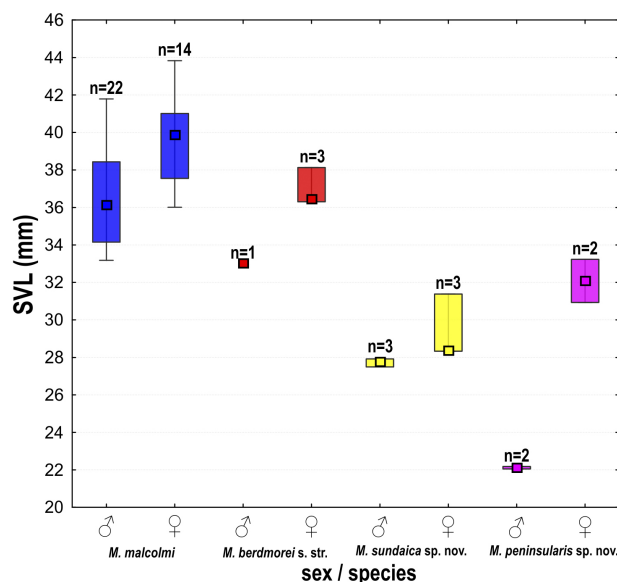


Figure 4. Boxplots of SVL (in mm) showing size variation among adult frogs in the *Microhyla berdmorei* species complex. Squares within each box represent the median, and boxes encompass the 75th and 25th quartiles; n indicates sample sizes. Box color corresponds to colors in Figures 1–5.

The four mOTUs are characterized by different adult body sizes, with the populations from the mainland Indo-Burma (including mOTU1 and mOTU2) being larger than the Sundaland lineages from the Thai-Malay Peninsula (including mOTU3 and mOTU4) (Fig. 4). Adult males of mOTU4 are the smallest, being reproductively active (calling) at a body size of 22.1–22.2 mm, which was previously not reported for the *M. berdmorei* species complex. At the same time, adult females of mOTU4 are larger (30.9–33.2 mm) than that of mOTU3 (28.3–31.4 mm), but much smaller than that of mOTU1–mOTU2 (36.0–43.8 mm). However, the small sample sizes of the mOTU2–mOTU4 specimens examined are not adequate to test for statistical significance of the observed differences in body size variation within the *M. berdmorei* species complex.

All examined characters exhibit normal distributions in all datasets. The univariate analysis revealed statistically significant differences between the members of the *M. berdmorei* species complex in body ratios (divided by SVL). The P-values associated to the univariate morphological comparisons among the four mOTUs are summarized in Table 5. Univariate analyses for both the male, female, and combined datasets showed significant differentiation in the SVL, RHL, REL, RSL, RIND, RIOD, R3FDD, and RIMTL between the four mOTUs (Table 5).

PCA plots revealed that all four mOTUs generally show little to no overlap in the morphospace (Fig. 5). PCA1 accounted for 36.72% of the total variance and loaded most heavily on SVL and RHL. PCA2 accounted for 27.85% of the total variance and loaded most heavily on RIND and R3FDD. More details on the PCA results can be found in Table S7. Overall, the morphometric data was distributed in two large clusters that separated the large-bodied specimens (which belong to mOTU1 and mOTU2) and the small-bodied specimens (which belong to mOTU3 and mOTU4). Given their very low sample sizes that might underestimate the true variation found among natural populations, the inferred morphospace for mOTU2 (n = 4) and mOTU4 (n = 4) on the PCA must be interpreted cautiously.

Systematics

The updated mtDNA-genealogy presented in our work is consistent with the results of Gorin et al. (2020) and Kundu et al. (2021). In parallel, the ddRAD-seq analysis supports that the mitochondrial lineages correspond to equivalent divergence in the nuclear genome. All the available molecular evidence thus supports that *M. berdmorei* as currently understood (sensu lato) represents a species complex composed of four deeply-diverged, geographically circumscribed lineages (indicated above as mOTU1–4; see Fig. 2B). The phylogenetic relationships between these lineages are generally well supported in both mitochondrial and nuclear analyses, which recover two clades, one corresponding to the mainland populations (mOTU1 and mOTU2), and one corresponding to Sundaland populations (mOTU3 and mOTU4). The BDNF-gene polymorphism also provide evidence for nuclear diagnosticity, but only between mOTU3 and mOTU4, and mOTU1+ mOTU2 (Fig. 2A).

The 16S divergence among these lineages (p = 1.5%–3.8%) is on the verge of the 3.0% threshold that is traditionally used to infer species status in anuran biodiversity surveys (Vences et al. 2005a,

Table 5. Resulting p values from univariate morphological analyses comparing the geographic populations of the *Microhyla berdmorei* species complex: Vietnam, central and northern Indochina, peninsular Thailand (OTU1, *M. malcolmi*), India, Bangladesh and Myanmar (OTU2, *M. berdmorei* sensu stricto), peninsular Malaysia, Sumatra and Borneo (OTU3, *Microhyla sundaiica* sp. nov.), and peninsular Thailand and Malaysia (OTU4, *Microhyla peninsularis* sp. nov.). Characters in bold are considered statistically significant. All characters were examined using Student's T Tests.

Dataset	Species pair	SVL	RHL	RHW	REL	RSL	RN-EL	RIND	RIOD	UEW	R3FDD	RL-AL	REFL	RHLL	RTL	RFL	RIMTL
Combined	mOTU1 vs mOTU2	0.2694	0.0001	0.8905	0.0971	0.8229	0.2339	0.0022	0.4103	0.8556	0.0034	0.0795	0.7997	0.1809	0.9942	0.2092	0.0193
	mOTU1 vs mOTU3	0.0000	0.0112	0.7947	0.4571	0.6449	0.9492	0.0000	0.0001	0.2113	0.0000	0.3325	0.3503	0.0474	0.0548	0.0445	0.0028
	mOTU1 vs mOTU4	0.0000	0.0002	0.1642	0.8643	0.7041	0.6418	0.0000	0.1014	0.7932	0.0002	0.9734	0.0498	0.0474	0.0699	0.1307	0.8873
	mOTU2 vs mOTU3	0.0002	0.0620	0.6924	0.2031	0.2432	0.1278	0.1525	0.0064	0.1665	0.1302	0.1538	0.4937	0.6325	0.0296	0.7568	0.9362
Males	mOTU2 vs mOTU4	0.0285	0.4491	0.2640	0.3389	0.5539	0.0844	0.2111	0.3287	0.8161	0.2745	0.2121	0.1198	0.4539	0.0213	0.8836	0.3445
	mOTU3 vs mOTU4	0.5631	0.1110	0.2559	0.6052	0.9872	0.5800	0.9840	0.5033	0.6666	0.3393	0.4440	0.1853	0.6081	0.7115	0.9031	0.1999
	mOTU1 vs mOTU2	0.1904	0.0009	0.8939	0.0171	0.9614	0.8366	0.0260	0.5719	0.9950	0.0652	0.1260	0.9774	0.3394	0.8444	0.0677	0.0046
	mOTU1 vs mOTU3	0.0000	0.0219	0.9270	0.1126	0.8454	0.9423	0.0002	0.0541	0.2754	0.0033	0.7546	0.5025	0.2243	0.1599	0.2237	0.0500
Females	mOTU1 vs mOTU4	0.0000	0.0002	0.4191	0.8282	0.2355	0.4778	0.0001	0.0008	0.6025	0.0042	0.2756	0.2244	0.1348	0.1174	0.0214	0.1565
	mOTU2 vs mOTU3	0.0021	0.4421	0.8042	0.3516	0.8670	0.5074	0.8553	0.6459	0.5574	0.9226	0.2028	0.7762	0.6901	0.0464	0.0826	0.4435
	mOTU2 vs mOTU4	0.0051	0.2822	0.7216	0.3541	0.0443	0.0237	0.3222	0.1786	0.8938	0.0603	0.0572	0.6867	0.9256	0.4021	0.7851	0.4690
	mOTU3 vs mOTU4	0.0001	0.4086	0.5439	0.4852	0.0436	0.1045	0.3588	0.1681	0.8427	0.9595	0.3039	0.6590	0.5787	0.3815	0.0477	0.8768
Females	mOTU1 vs mOTU2	0.0722	0.0278	0.3503	0.9551	0.6140	0.2686	0.0486	0.2637	0.9419	0.0295	0.0870	0.9791	0.2761	0.9075	0.9980	0.0653
	mOTU1 vs mOTU3	0.0000	0.1941	0.9411	0.5759	0.6925	0.9420	0.0013	0.0001	0.4671	0.0000	0.1916	0.6025	0.1103	0.2348	0.1333	0.0044
	mOTU1 vs mOTU4	0.0005	0.0516	0.2591	0.5993	0.3873	0.9718	0.0384	0.1514	0.8920	0.0207	0.3863	0.1854	0.1945	0.3628	0.6326	0.1149
	mOTU2 vs mOTU3	0.0030	0.1092	0.4635	0.1895	0.2508	0.3090	0.2265	0.0069	0.3971	0.0150	0.2589	0.4183	0.5211	0.1764	0.3231	0.3396
Females	mOTU2 vs mOTU4	0.0235	0.6279	0.2461	0.7384	0.6174	0.3534	0.6540	0.7015	0.9622	0.5810	0.0015	0.0961	0.5895	0.1416	0.7558	0.0558
	mOTU3 vs mOTU4	0.1856	0.1335	0.2395	0.9256	0.2874	0.9288	0.5223	0.0132	0.7496	0.0794	0.0135	0.0928	0.9576	0.9022	0.0343	0.0168

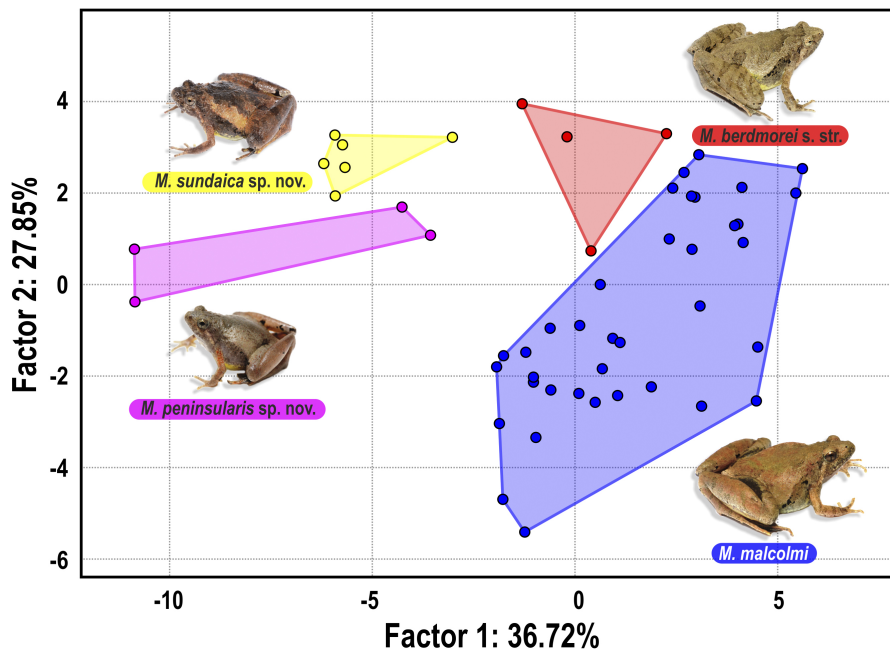


Figure 5. First and second factors of PCA built from 29 morphological characters measured in adult frog specimens of the *Microhyla berdmorei* species complex. Colors correspond to colors in Figures 1–4. Photographs by A. V. Trofimets, A. M. Bragin, P. Pawangkhanant, and N. A. Poyarkov.

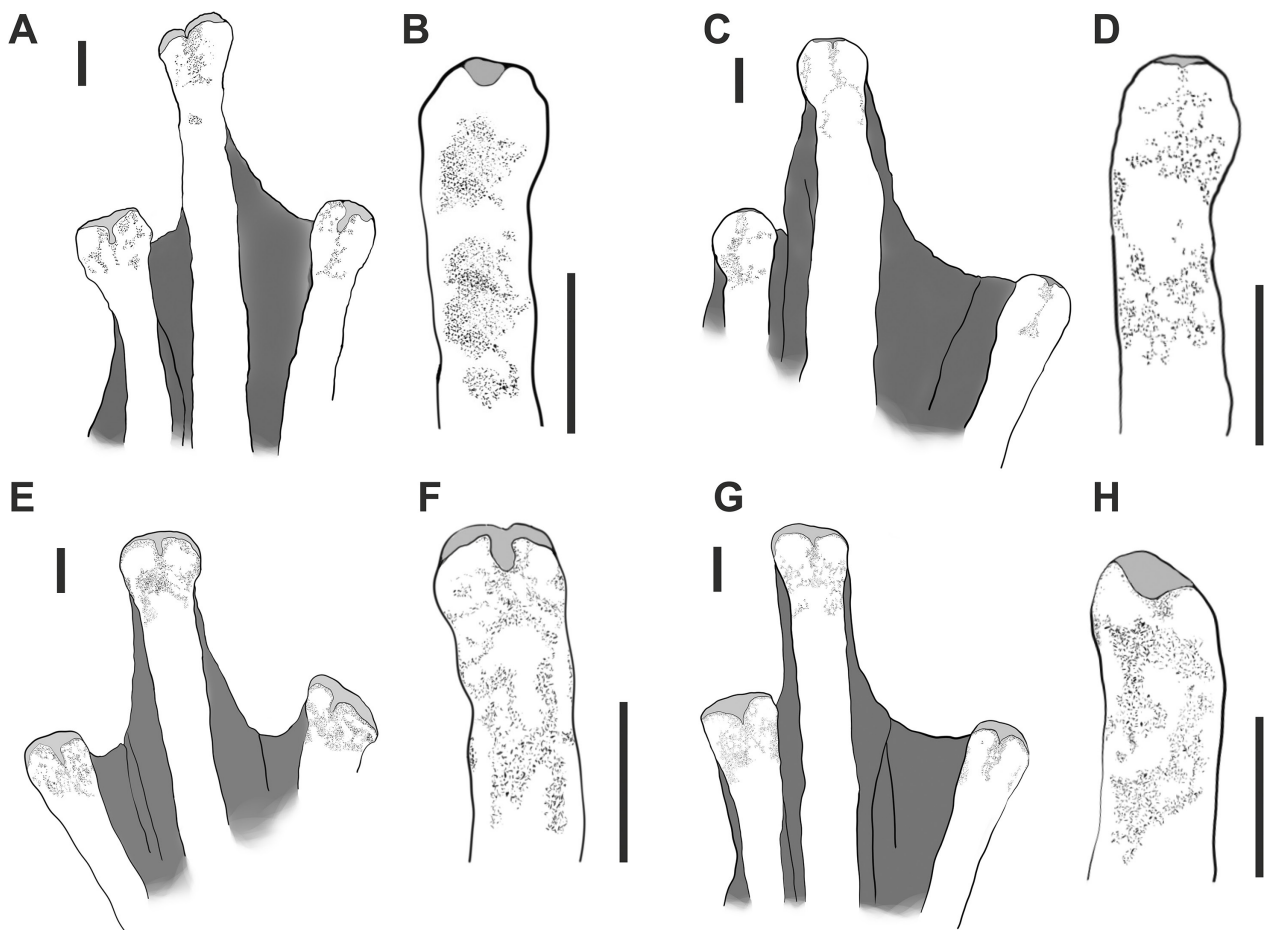


Figure 6. Dorsal aspects of fourth toes (A, C, E, G) and third fingers (B, D, F, H) of the *Microhyla berdmorei* species complex members. A, B *M. berdmorei* sensu stricto, ZMMU A-8005; C, D *M. malcolmi*, ZMMU A-7973; E, F *M. sundaica* sp. nov., ZMMU A-8011, holotype; G, H *M. peninsularis* sp. nov., ZMMU A-8016, holotype. Scale bar equals to 1 mm. Drawings by A. M. Bragin.

2005b; Vieites et al. 2009). However, this threshold is rather conservative and may under-estimate species diversity given that many lineages known to feature partial reproductive isolation bear substantially lower 16S distanc-

es (Dufresnes and Litvinchuk 2022). For instance, about half of the pairs of lineages with as little as ~1–2% of divergence at 16S investigated in Western Palearctic anurans turn out to be valid species (Dufresnes et al. 2021).

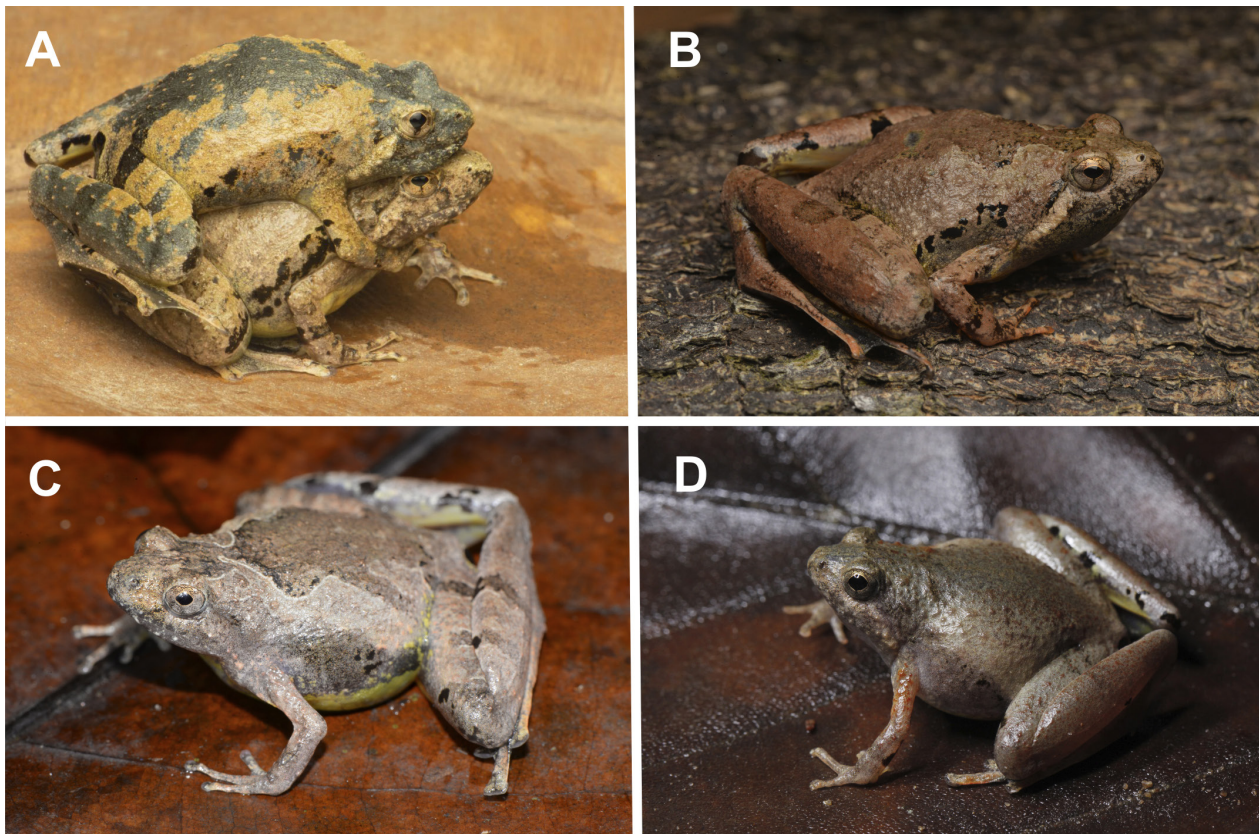


Figure 7. Members of the *Microhyla berdmorei* species complex in life. **A** *M. berdmorei* sensu stricto, MZMU A-8005 and MZMU A-8003 (a couple showing cephalic amplexus) from Aizawl, Mizoram State, India; **B** *M. malcolmi*, ZMMU A-7973 from Than To, Yala Province, Thailand; **C** *M. sundaica* sp. nov., ZMMU A-8011 (holotype) from environs of Sungai Tua Recreational Forest, Selangor State, Malaysia; **D** *M. peninsularis* sp. nov., ZMMU A-8016 (holotype) from Lam Plok Waterfall, Trang Province, Thailand. Photographs by: A. M. Bragin (A), N. A. Poyarkov (B), A. T. Aful (C), P. Pawangkhanant (D).

Accordingly, the lineages were dated to the Mio-Pliocene transition and earlier, which usually correspond to species-level divergence (Dufresnes and Litvinchuk 2022).

Furthermore, even though based on limited sampling for mOTU2–4, our morphological analyses uncovered significant morphological differentiation among the four lineages of the *M. berdmorei* complex (Figs 4–5). The mOTUs are differentiated in body size (Fig. 4) and body proportions (Fig. 5), with their respective differences broadly following their phylogenetic relationships. The distinction of these lineages is further corroborated by stable differences in coloration, pattern, and external morphology, which are summarized below. Finally, despite the limited number of recordings, we managed to analyze the main acoustic parameters of male advertisement calls for three out of the four mOTUs (mOTU1–3). Our analysis revealed consistent variations in temporal and power call parameters among mOTU1–3, as elaborated upon below.

Therefore, based on the cumulative molecular, bioacoustic and morphological evidence (see comparisons below, Figs 6–7; Table 6), we hypothesize that the four mOTUs of the *M. berdmorei* complex should be considered as four discretely diagnosable evolutionary entities that should warrant a taxonomic recognition. Moreover, given their old evolutionary age, we consider all of them as separate species.

The large-sized lineages mOTU1 and mOTU2 include populations from the mainland Indo-Burma, which until recently were defined as *M. berdmorei* sensu stricto by Garg et al. (2019), Gorin et al. (2020), and Kundu et al. (2021). In the present study, we demonstrate that there is a significant differentiation between the lineages mOTU1 from Indochina and mOTU2 from Myanmar, India, and Bangladesh. The lineages mOTU1 and mOTU2 likely diverged ca. 5.19 mya (Figs 2, S2); however, they are characterized by a moderate level of divergence in 16S rRNA gene sequences ($p = 1.76\text{--}2.02\%$ in the 16S rRNA gene; see Table 2). At the same time, these two lineages are well separated in morphospace (Figs 4, 5) and are diagnosed by stable differences in a number of morphological characters (see below; Table 6). As the type locality of *M. berdmorei* (Blyth, 1856) is located in Bago Region, Myanmar, this nomen is therefore applicable to mOTU2. Two of the molecularly examined populations are located in proximity to the type locality of *M. berdmorei* (localities 43 and 44, see Fig. 1). The type locality of *Callula natatrix* Cope, 1867, in Yangon Region, Myanmar (see Fig. 8) is also located within the mOTU2 range, suggesting synonymy of the latter nomen with *M. berdmorei* (Fig. 1), what also agrees with morphological data (see below).

The lineage mOTU1 is widely distributed across all of Indochina, including Vietnam, Laos, Cambodia, Thailand, including the Thai-Malay Peninsula; it also pene-

Table 6. Morphological diagnostics of the *Microhyla berdmorei* species group members.

Species	<i>M. berdmorei sensu stricto</i>	<i>M. malcolmi</i>	<i>M. peninsularis sp. nov.</i>	<i>M. sundaica sp. nov.</i>	<i>M. darevskii</i>	<i>M. picta</i>	<i>M. pulchra</i>
SVL (males, mm)	33.0	33.2–41.8	22.1–22.2	27.5–27.9	27.0–32.6	25.2–30.1	23.0–32.0
SVL (females, mm)	36.3–38.1	36.0–43.8	30.9–33.2	28.3–31.4	?	27.2–33.4	28.0–36.5
Body habitus	Slender	Slender	Stocky	Stocky	Stocky, flattened	Stout	Stocky
Snout in lateral profile	Obtusely pointed	Obtusely pointed	Obtusely pointed	Rounded	Rounded	Rounded	Obtusely pointed
Skin on dorsum	Smooth, small tubercles	Smooth, small tubercles	Smooth, small tubercles	Smooth, small tubercles	Slightly tubercular	Tubercular or slightly warty	Smooth
F1 vs. F2	F1 < 1/2 F2	F1 < 1/2 F2	F1 > 1/2 F2	F1 > 1/2 F2	F1 > 1/2 F2	F1 < 1/2 F2	F1 < 1/2 F2
Finger disks	present (weak)	present (weak)	present	present	absent	absent	absent
Dorsomedial grooves on finger disks	present (weak)	present (weak)	present	present	absent	absent	absent
Toe disks	present	present	present	present	present (weak)	absent	absent
Dorsomedial grooves on toe disks	present (weak)	present (weak)	present	present	present	absent	absent
Metatarsal tubercles	2	2	2	2	2	2	2
Superciliary tubercles	absent	absent	absent	absent	absent	absent	absent
Light vertebral line	absent	absent	absent	absent	absent	absent	absent
Tibiotarsal articulation reaches	Well beyond snout	Well beyond snout	Well beyond snout	Well beyond snout	Well beyond snout	Eye level	To snout or just beyond
Toe webbing formula	i1-1iii1-2iii1-2iv2-1v	i1-1iii1-1iii1-1iv1-1v	i1-1iii1-2iii1-1iv2-1v	i1-1iii1-2iii1-1iv1-1v	i1-1iii1-1iii1-1iv1-1v	i2-2 ⁱⁱⁱ 1 ^{1/4} -2 ⁱⁱⁱ 2 ⁱⁱⁱ 2 ^{3/4} -3 ^{3/4} iv4-2 ^{1/2} v	i1 ^{1/2} -2ii1-3iii2-3 ^{1/4} iv3 ^{1/2} -2v
Distributions	Northeastern India, Bangladesh, Myanmar	Southern Yunnan (China), Vietnam, Laos, Cambodia, Thailand, West Malaysia (Perlis)	Southern peninsular Thailand (Trang), northern peninsular Malaysia	Peninsular Malaysia, Sabah (East Malaysia), Sumatra and Kalimantan (Indonesia)	Vietnam (Kon Tum Province)	South Central Coast Vietnam	China, Vietnam, Laos, Cambodia, Thailand, Myanmar?
Sources	Blyth (1856); Cope (1867); our data	Cochran (1927); Taylor (1934); our data	our data	our data	Poyarkov et al. (2014); our data	Schenkel (1901); Poyarkov et al. (2014); our data	Hallowell (1861); Poyarkov et al. (2014); our data

trates to the northernmost portion of Peninsular Malaysia (Perlis State, locality 32, see Fig. 1); this lineage is expected to occur in the southernmost Yunnan Province of China (Yang and Rao 2008; Fei et al. 2009, 2010, 2012; Li et al. 2019). Two nomina were earlier proposed for the populations within the range of mOTU1: *M. malcolmi* Cochran, 1927, and *M. fowleri* Taylor, 1934 (see Figs 9, 10). In our sampling, population 23 is located in close proximity of the type locality of *M. malcolmi* (in Pak Chong, Nakhon Ratchasima Province, Thailand), and population 25 originates from the same province as the type locality of *M. fowleri* (in Chiang Mai Province, Thailand; Fig. 1). Therefore, the nomen *M. malcolmi* Cochran, 1927, has priority for mOTU1. We herein revalidate this taxon as a valid species, and suggest *M. fowleri* as a junior synonym.

The lineages mOTU3–4 have much smaller adult body sizes than typically reported for “*M. berdmorei*” populations (Fig. 4; Table 3). The lineage mOTU3 has an extensive distribution covering Peninsular Malaysia, Sumatra, and Borneo, while the lineage mOTU4 is restricted to southern Peninsular Thailand (Trang Province) and northern Peninsular Malaysia (Terengganu State) (Fig. 1). The distribution of mOTU3, mOTU4, and (partially) mOTU1 (subclade A3) overlaps in southern Thailand and Peninsular Malaysia, but these were not found in sympatry (Fig. 1). 16S divergence between mOTU3 and mOTU4 is rather shallow ($p = 1.49\%–2.48\%$), with their divergence from mOTU1–2 moderately higher ($p = 2.07\%–3.79\%$; see Table 2). Their estimated age to the late Miocene (ca. 5.69 mya; Figs 2, S2) are comparatively older than the split between mOTU1 and mOTU2. In parallel, the mOTU3 and mOTU4 can be clearly diagnosed from each other and from mOTU1–2 (Figs 6–7; Table 6), based on morphology (both in body size and proportions), coloration, and diagnostic characters such as the degree of foot webbing

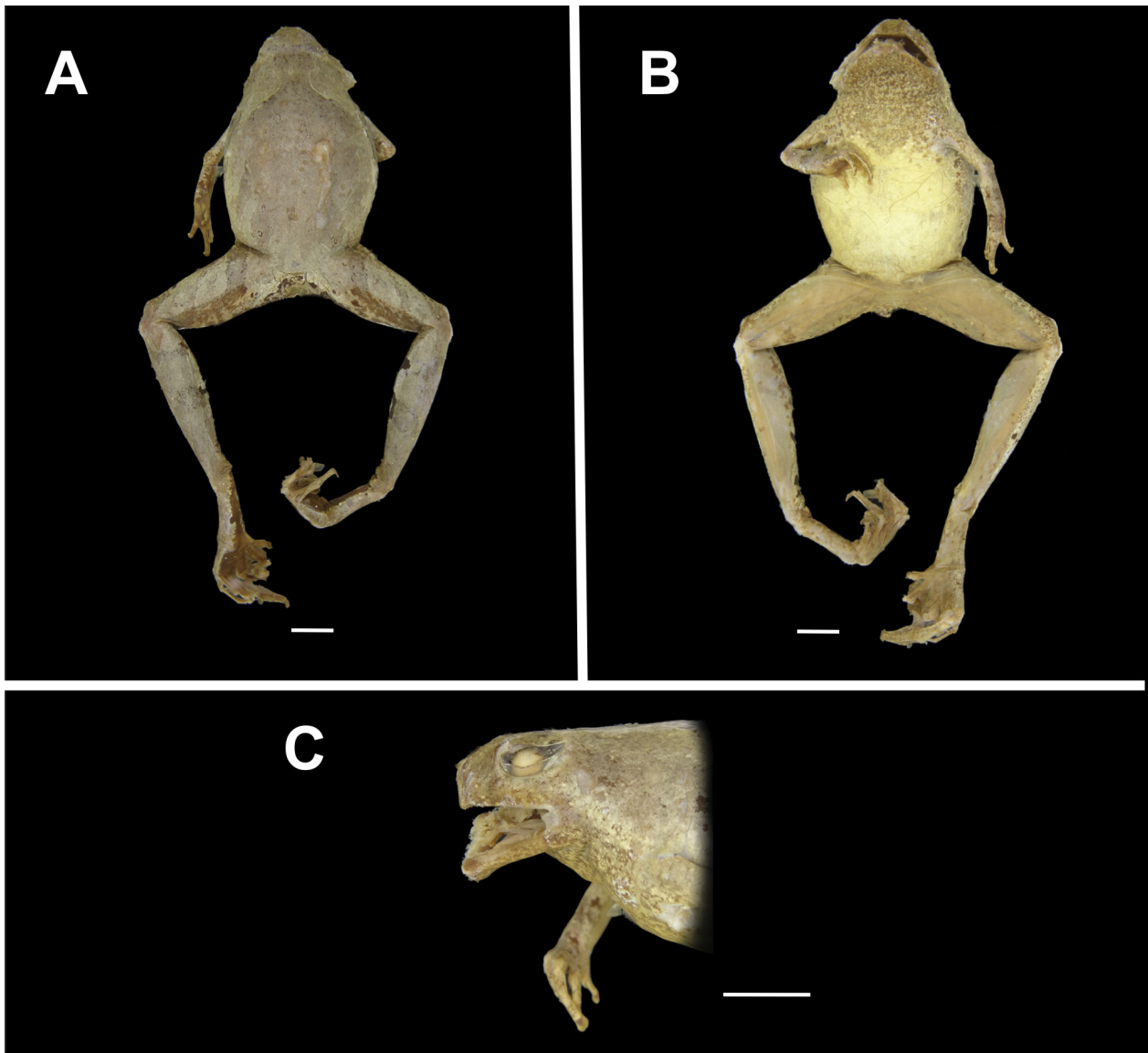


Figure 8. *Microhyla berdmorei* sensu stricto in preservative – specimen MCZ A-1587 (syntype of *Callula natatrix* Cope, 1867) from “Near Rangoon, Burmah” (now environs of Yangon Region, Myanmar). **A** Dorsal aspect; **B** ventral aspect; **C** lateral view of head. Scale bar equals 3 mm. Photographs by Harvard University, USA (<http://mczbase.mcz.harvard.edu/guid/MCZ:Herp:A-1587>).

and toe disk development. Therefore, as previously no nomina are available for the populations of the *M. berdmorei* complex from the Sundaland, we formally describe mOTU3 and mOTU4 as two new species below.

Microhyla berdmorei species complex

Microhyla berdmorei (Blyth, 1856)

Figures 6A, B, 7A, 8, 9, 10A; Tables 3, 6, S2

Common name. Berdmore’s narrow-mouthed frog.

Synonymy and chresonymy.

Engystoma berdmorei Blyth, 1856 “1855”: 720. Type(s): not stated.

Type locality: “Schwe Gyen” (now Shwegyin) on the Sitang River, “Pegu” (now Bago Region), Myanmar; Sclater (1892: 23).

Callula natatrix Cope, 1867: 192. Syntypes: MCZ 630 (= MCZ 1587), and MCZ A-153454-57 (apparently renumbered), according to Barbour and Loveridge (1929) and Harvard University, USA data (<http://mczbase.mcz.harvard.edu>). Type locality: “Near Rangoon, Burmah” (now Yangon Region, Myanmar); Li et al. (2019: 568).

Diplopelma (Engystoma) berdmorei — Günther (1868: 146).

Diplopelma pulchrum Theobald (1868: 83, in part) (non *Engystoma pulchrum* Hallowell, 1861, now *Microhyla pulchra*; misidentification).

Diplopelma berdmorei — Theobald (1873: 112).

Microhyla berdmorei — Boulenger (1882: 166). Incorrect subsequent spelling.

Microhyla (Engystoma) berdmorei — Mason (1882: 292).

Microhyla (Engystoma) berdmorei — Boulenger in Mason (1882: 500).

Microhyla berdmorei — Bourret (1942: 509, in part); Frank and Ramus (1995: 90, in part); Dutta (1997: 58–59, in part); Das and Dutta (1998: 64); Chanda (2002: 36–39, in part); Choudhury (2002: 277, in part); Devi and Shamungou (2006: 317–324); Sarkar and Ray (2006: 291, in part); Das and Dutta (2007: 154–181); Wogan et al. (2008: 88, in

part); Dinesh et al. (2009: 302; in part); Mahony et al. (2009: 80–94); Mathew and Sen (2010: 65–66); Sengupta et al. (2010: 30); Bjiu et al. (2019: 103); Garg et al. (2019: 15, in part); Li et al. (2019: 566, in part); Nguyen et al. (2019: 549–580, in part); Ahmad and Mim (2020: 36–71); Gorin et al. (2020: 1–47, in part); Hakim et al. (2020: 1239–1268); Poyarkov et al. (2020c: 1525–1558, in part); Gorin et al. (2021: 97, in part); Kundu et al. (2021: 1586–1591, in part); Zug (2022: 30, in part); Raj et al. (2023: 57–61); Dinesh et al. (2023: 7, in part); Frost (2024, page “*Microhyla berdmorei*” in part).

Microhyla (Microhyla) berdmorei — Dubois (1987: 3).

Microhyla butleri (non *Microhyla butleri* Boulenger, 1900) — Lalrem-sanga et al. (2007: 348; misidentification).

Microhyla sp. — Hasan et al. (2012: 162–172).

Types. Not stated in the original publication; ZSIC 9718–20 (not examined by us) were listed as syntypes by Sclater (1892), although Blyth (1856) provided measurements for a single specimen. Garg et al. (2019) discussed the confusing status of the type specimens; see discussion below.

Revised diagnosis. *Microhyla berdmorei* sensu stricto is characterized by a combination of the following morphological features: (1) large body size (SVL 33.0 mm in a male, 36.3–38.1 mm in females), with moderately slender and triangular body habitus; (2) head wider than long; (3) dorsal skin shagreened with occasional small tubercles; (4) snout rounded in dorsal and ventral views, obtusely pointed in lateral view; (5) first finger shorter than half of the second finger length; (6) finger tips with weak disks bearing wide and shallow dorsomedial grooves; (7) toes with distinct disks, each bearing a narrow and deep dorsomedial groove; (8) tibiotarsal articulation of the adpressed limb extending far beyond snout; (9) toe webbing reaching disks on all toes except toe IV; webbing formula: $1I-1II1-2III1-2IV2-1V$; (10) throat and chin dusty gray to almost black in breeding males; belly yellowish-white; (11) dorsal surfaces of forelimbs and hindlimbs with narrow prominent crossbars, up to 5–6 crossbars on thighs; (12) dark-brown patch above cloacal opening inverted-U-shaped or crescent-shaped; dark blotches on both sides of cloaca; (13) dorsum generally with distinct olive-brown “teddy-bear”-pattern edged with light brown; dark dorsal markings may be indistinct or completely absent; (14) body flanks with black irregular spots and blotches; (15) broad olive-gray lateral band extending from armpit to middle of trunk; (16) light postocular stripe yellowish-beige with no dark edging; (17) reddish spots on dorsum and dorsal surfaces of hindlimbs absent; (18) iris with black stripe below the pupil.

Material examined. In this study, we used morphological data from five specimens of *M. berdmorei* sensu stricto from India (see Table S2 for details).

Description of the voucher specimen MZMU A-8003 (Fig. 9). An adult female in a good state of preservation. Body size large (SVL 36.4 mm; other measurements are presented in Table S2). Body habitus slender, triangular, and dorsoventrally flattened (Fig. 9). Head triangular in dorsal view; wider than long (HW/HL ratio 1.19). Snout

comparatively short and protruding (SL/HL ratio 0.46), rounded in dorsal view (Fig. 9A), obtusely pointed in profile, noticeably extending beyond the edge of the lower jaw (Fig. 9E). Eyes large, protruding in dorsal and lateral views, significantly shorter than the snout (EL/SL ratio 0.71), slightly longer than interorbital distance (IOD/EL ratio 0.90). Canthus rostralis distinct, rounded; loreal area slightly concave. Nostrils oval-shaped, with lateral orientation, situated below the canthus rostralis, slightly closer to tip of snout than to eye. Interorbital distance greater than internarial distance (IND/IOD ratio 0.86). Upper eyelid length less than the interorbital distance (UEW/IOD ratio 0.79). Tympanum concealed, supratympanic fold indistinct, marked by a series of low tubercles (Fig. 9E). Tongue slender, rounded, free for the posterior four-fifths of its length; vomerine teeth absent. Eggs seen through the incision on the left lateral side of belly; eggs small, rounded, ca. 1.3–1.5 mm in diameter, pigmented (Fig. 9B).

Forelimbs short and slender (Fig. 9A, B); lower arm elongated and thin (LAL/FLL ratio 0.85), hand less than half of forelimb length (HAL/FLL ratio 0.48). Fingers slender and elongated; finger webbing or skin fringes absent. First finger well-developed, notably less than half of the second finger length (Fig. 9D); the relative finger length formula: $I < II \leq IV < III$. Fingertips rounded, slightly expanded into disks notably narrower than the basal phalanges of the respective fingers. Finger tips lacking peripheral grooves bearing a wide and shallow median notch on the dorsal surface of each finger (Fig. 6B). Finger tips almost equal in width, with the first finger tip slightly narrower. Subarticular tubercles on fingers distinct, large, rounded, and protruding; the distal subarticular tubercle on the fourth finger less distinct. The subarticular tubercle formula: 1, 1, 2, 2 (Fig. 9D). Two metacarpal tubercles: inner metacarpal tubercle distinct, protruding, rounded in shape; outer metacarpal tubercle rounded and flattened, its diameter subequal to the diameter of inner metacarpal tubercle (OPTL/IPTL ratio 0.89).

Hindlimbs long, slender, almost four times longer than the forelimbs (HLL/FLL ratio 3.85). Thighs muscular, massive (Fig. 9B), shanks elongated and slender, comprising approximately one-third of the hindlimb length (TL/HLL ratio 0.35). When the limbs are positioned at the right angle to the body, the heels significantly overlap. Tibiotarsal articulation of the adpressed limb extends well beyond the tip of the snout. Foot length comprises more than one-third of the hindlimb length, being significantly shorter than the tibia (FL/HLL ratio 0.31, TL/FL ratio 1.16). The relative toe lengths: $I < II < V \leq III < IV$. Shanks smooth, inner tarsal fold absent. Tips of all toes distinctly widened into round disks, notably wider than the finger tips (4FDD/3FDD ratio 1.75). Toe webbing fully developed, reaching the disks on all toes except the toe IV; webbing formula: $1I-1II1-2III1-2IV2-1V$ (Fig. 6A). Subarticular tubercles on toes distinct, rounded, slightly protruding, subarticular tubercle formula: 1, 1, 2, 3, 2 (Fig. 9D). Internal metatarsal tubercle of moderate size, slightly elongated, with indistinct margins, comprising

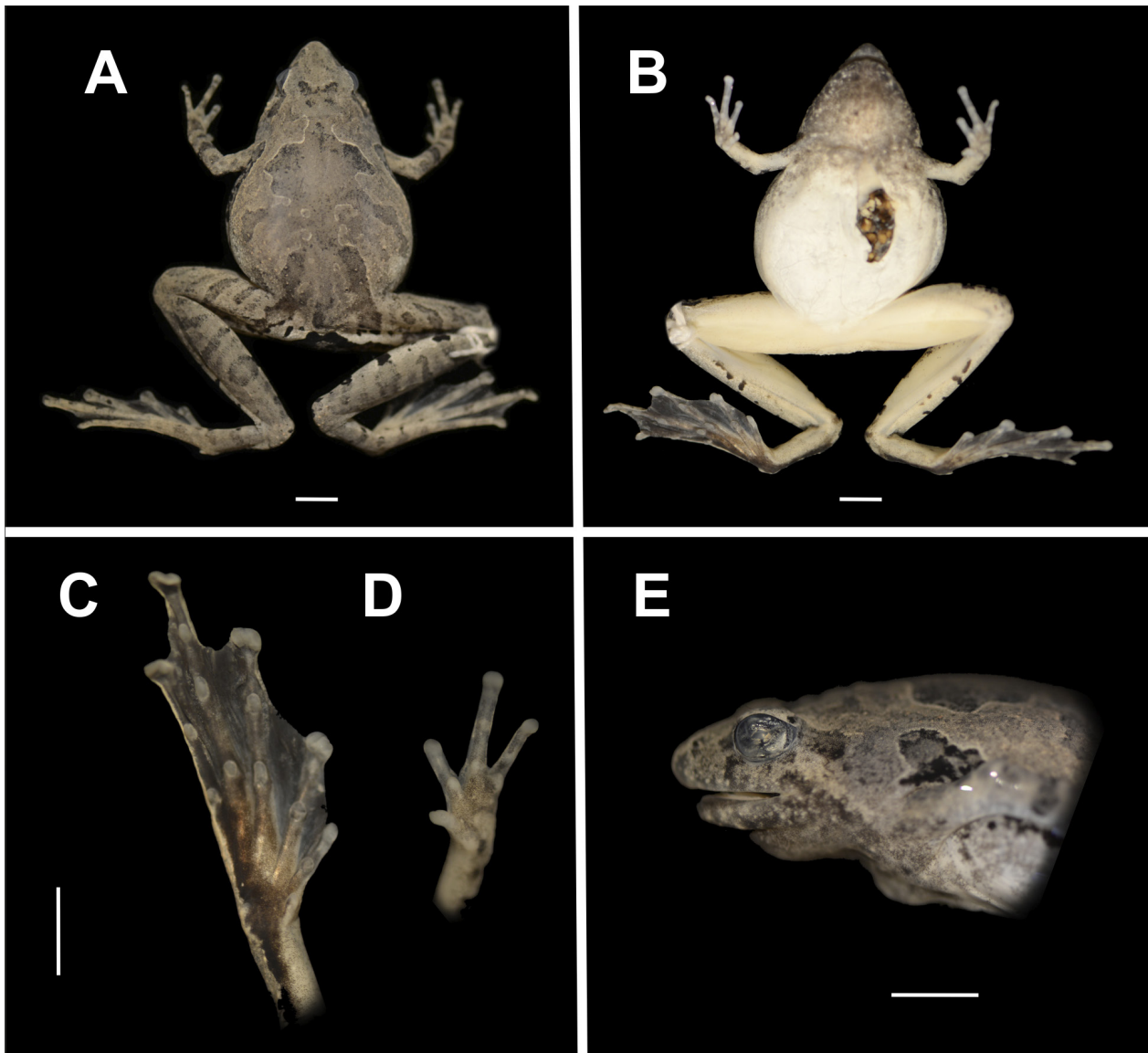


Figure 9. *Microhyla berdmorei* sensu stricto in preservative – specimen MZMU A-8003 (adult female) from Aizawl, Mizoram State, India: **A** Dorsal aspect; **B** ventral aspect; **C** plantar view of the right foot; **D** volar view of the left hand; **E** lateral view of head. Scale bar equals 3 mm. Photographs by A. V. Trofimets.

less than half the length of the first toe (IMTL/1TOEL ratio 0.36, Fig. 9C). Outer metatarsal tubercle small but distinct, rounded, prominent with well-defined margins, subequal to the length of inner metatarsal tubercle (OMTL/IMTL ratio 0.94, Fig. 9C).

Skin on dorsum shagreened, with rare small tubercles getting denser laterally (Fig. 7A). Dorsal surfaces of forelimbs almost smooth, with the exception of tiny tubercles present on forearms. Dorsal surface of hindlimbs with small tubercles sparsely scattered on thighs and shanks (Fig. 9A). Upper eyelid smooth. Body flanks smooth, numerous small warts around the tympanal region. Ventral sides of body and limbs completely smooth (Fig. 9B). Cloacal opening unmodified, with posterior orientation.

Coloration in life. Dorsum in life olive-brown with a bronze tint laterally with a dark-brown “teddy-bear” pattern (see Rakotoarison et al. 2017) with irregular borders (Fig. 7A). Dark-brown triangular interorbital bar located

between the posterior parts of upper eyelids continues posteriorly, sharply narrowing at the level of head base and broadening at the scapular area. A pair of dark-brown blotches edged with beige form a trapezoidal dark marking around the cloacal opening. A yellowish-beige light postocular stripe running from the posterior corner of the eye to the axilla (Fig. 7A).

Body and head flanks slightly darker than the lateral sides of the dorsum. Snout olive-brown lacking dark markings. Broad dark olive-gray band running posteriorly from the eye. Upper jaw dark-brown with a few irregular light-brown or cream spots below the eye. Narrow cream stripe running from the posterior corner of the eye to the axilla. Except for the upper arm, limbs dorsally with indistinct brownish crossbars and spots: two crossbars visible on lower arms, three crossbars on thighs and shanks. Fingers and toes with brown transverse dorsal bars.

Belly and chest yellowish-white, with a few irregular grayish spots in chest area (Fig. 7A). Throat and chin

with dense dark-gray mottling, which gets darker along the edges of mandible and mouth corners. Ventral surfaces of limbs beige to bluish-gray lacking dark markings (Fig. 9C,D); feet ventrally with dark-brown marking extending from the tibiotarsal joint to the ventral surfaces of toes and toe webbing (Fig. 9C). Iris bronze with a distinct vertical dark stripe ventrally. Pupil round, black, outlined with a thin golden circle.

Coloration in preservative. After two years in preservative, the pattern described above generally remains unchanged (Fig. 9). Dorsal background color faded to light-gray, and the dark dorsal markings became less discernible. The characteristic dark spot above the cloacal opening, the “teddy-bear” pattern, and other dark markings remain visible. Limbs fade to yellowish-gray, but the dark crossbars on the limbs remain visible. Ventral surfaces fade to light-beige; however, the dark markings on the chin still remain notable as brownish-gray mottling.

Variation. The examined individuals are overall quite similar in appearance. Differences in size and body proportions are provided in Tables 4 and 5. In females, the body length (SVL) ranges from 36.3 to 38.1 mm ($n = 3$); the single examined male had a smaller body size (SVL 33.0 mm). Dorsal background coloration of the examined specimens varied from olive-brown to yellowish-brown. The male specimen had a notably darker chin than the examined females (Fig. 7A).

Etymology. The species name “*berdmorei*” was given in honor of Captain Major Thomas Matthew Berdmore (1811–1859), a British officer and naturalist who was stationed in Myanmar during the mid-19th century. M. T. M. Berdmore was famous for the collection of numerous animal specimens, including this particular species of frog. Recommended common names: “Berdmore’s narrow-mouthed frog” (English); “Nhái bầu Béc-mơ” (Vietnamese); “uzkorot Berdmora” (узкорот Бердмора, Russian); “Changpîng” (Mizo; literally meaning “spindle frog”); “Eung mae nao Pama” (อึ่งแม่หนาวพม่า, Thai).

Distribution. Based on our definition of *M. berdmorei* sensu stricto, the actual range of this taxon (Fig. 1) is restricted to: India (northeastern part of the country: Meghalaya, Assam, Tripura, and Mizoram states), Bangladesh (central, northeastern, and southeastern parts of the country), and Myanmar (northwestern and central parts of the country). The earlier records of the occurrence of *M. berdmorei* in Indochina, Malaysia, and Indonesia refer to other species of the *M. berdmorei* complex described below.

Natural history notes. *Microhyla berdmorei* sensu stricto inhabits various types of moist evergreen forests, including monsoon and perennial rainforest types. It is generally associated with hilly regions and is often found near streams; it also occurs in secondary forests. Specimens of this species are active day and night, often hiding in the leaf litter on the forest floor. When disturbed, they make extraordinary long and vigorous jumps to escape. In As-

sam State, India, breeding activity typically occurs in still pools between October and November (Garg et al. 2019; IUCN 2022). The noisy rasping call of *M. berdmorei* sensu stricto can be heard at night from beside forest pools; we have observed specimens of this species displaying cephalic amplexus (Fig. 7A). In India, Garg et al. (2019) recorded specimens from thickly vegetated swampy areas near the water bodies, either inside secondary forests or adjacent to human settlements. In Lawachara N. P., Bangladesh, Hakim et al. (2020) found *M. berdmorei* on trails, roads, and leaf litter in mature forests, degraded forests, tea plantations, and village habitats. *Microhyla berdmorei* coexists with *M. mymensinghensis* Hasan et al., 2014 in the northeastern (Dinajpur, Parbatipur) region of Bangladesh (Hasan et al. 2014). This species was found either in the grass below large trees, referred to as “Lendi Korui” by the locals, or in expansive fields with some vegetation and somewhat damp and loose soil. Indigenous to the region, this species is commonly referred to as “Boro Laubichi Bang”, and its diet mostly includes ants and other small insects (Hasan et al. 2014). In Mizoram, India, the species prefers waterbodies with sandy to gravel bottoms for breeding (Raj et al. 2023).

Tadpole. Raj et al. (2023) presented a detailed description of the larval morphology of *M. berdmorei* from Aizawl, Mizoram, India. Tadpoles at Gosner stage 34 reach 20–21 mm in length; at Gosner stage 39 they reach 27–28 mm in length. At Gosner stage 37, body large, oval-shaped in dorsal view; body length comprises 37% of total length; snout broad and truncate in dorsal view, acutely rounded in lateral view; eyes with lateral orientation; eye-nostril distance comprises 69% of eye-snout distance; interorbital distance ca. three times greater than internarial distance; spiracle large, medial, located on ventral surface; spiracle-snout distance comprises 83% of body length; vent tube opening medial, reaching ventral fin edge; ventral tail fin deeper than dorsal tail fin, reaching its maximal height at tail mid-length; caudal musculature comprises 40% of tail height; tail tip sharply pointed, flagellated. Oral disc terminal, comprising a half of interorbital distance in width; lacking papillae or keratinized structures; a U-shaped medial notch protrudes from the mouth between the two semicircular labial flaps (Lalremsanga and Muansanga 2022; Raj et al. 2023). In life, head, body, and caudal musculature translucent and white with numerous tiny melanophores; posterior parts of body darker due to pigmentation of inner integument; ventrally milky white and transparent with gut coils visible; few large melanophores present on both tail fins; smaller melanophores present on tail musculature. Tadpoles of *M. berdmorei* are lentic suspension feeders.

Advertisement call. The male advertisement call of *M. berdmorei* represents a series of short rasping sounds resembling the sound of a ratchet. In an unpublished doctoral thesis, Lalremsanga (2011: 102) provided a description of the advertisement call for the *M. berdmorei* population from Mizoram, Northeast India. The call series consisted of one to seven calls emitted at a 3 s interval; a single call

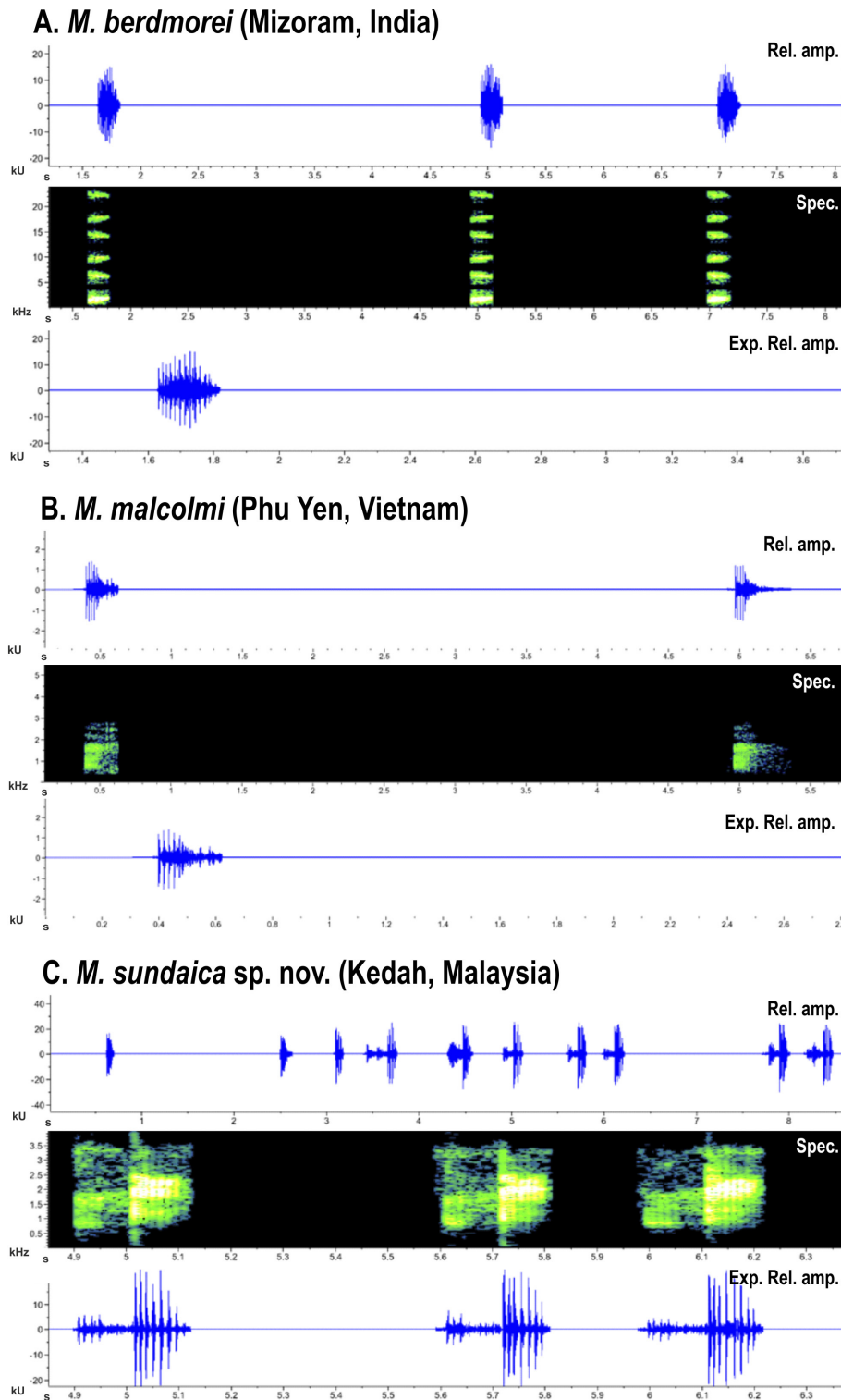


Figure 10. Male advertisement call of the *M. berdmorei* species complex members, showing a 8 s waveform of relative amplitude (Rel. amp., above), the corresponding spectrogram of the same call (Spec., middle), and expanded 3.6 s waveform of relative amplitude of the same call (Exp. Rel. amp., below) for each species. **A** *M. berdmorei* from Aizawl, Mizoram State, India; **B** *M. malcolmi* from Song Hinh Forest Reserve, Phu Yen Province, Vietnam; **C** *M. sundaica* sp. nov. from Gunung Jerai Mt., Kedah State, Peninsular Malaysia.

series lasted for 1.4–1.6 s. Each call consisted of 7–12 pulses and lasted for 0.2 s at an interval of 0.06 s. The amplitude of the call increased slowly and reached a peak in the middle, which then decreased slowly until the end. The frequency spectra ranged between 1484 and 2046 Hz, with the dominant frequency being 1677 Hz.

Our recording of male advertisement call series of *M. berdmorei* from Aizawl, Mizoram State, India, consisted of several calls (2–5; average 3.6 ± 1.2) emitted at a 2.5 ± 0.2 s (1.47–3.20 s) interval. A single call lasted for 0.20 ± 0.07 s (0.12–0.33) on average. Each call consist-

ed of 11 ± 2.0 (9–13) pulses emitted at an interval of 0.06 s. The call's amplitude increased slowly and reached a peak in the middle of the call, after which it gradually decreased; thus, each call's relative amplitude profile has a symmetrical shape (Fig. 10A). The peak frequency of a call comprised 1892 ± 82 Hz (1781–1969 Hz), which is notably higher than the earlier estimates of Lalremsanga (2011).

Comparisons. *Microhyla berdmorei* sensu stricto can be distinguished from all other known *Microhyla* species

currently known from South and Southeast Asia by its complete foot webbing, extending well beyond the first subarticular tubercle on either sides of toe IV and reaching up to the disks on the remaining toes (vs. rudimentary to medium foot webbing in all other species); by terminal phalanges of toes Y-shaped (vs. simple, knobbed, or T-shaped in all other species; see Garg et al. 2019); and by toe tips enlarged into disks with dorso-terminal grooves (vs. almost absent). This species can be differentiated from its close genetic congener *M. darevskii* by finger I length less than half of finger II length ($F1 < \frac{1}{2}F2$ vs. $F1 > \frac{1}{2}F2$); by weak disks present on fingers (vs. finger disks totally absent); by ventral color lightly colored, yellowish-white with irregular grayish spots (vs. no yellow color on groin and belly); by pattern on flanks and shanks consisting of brown or black irregular spots and blotches (vs. absent); by iris coloration bronze with a distinct dark vertical stripe below the pupil (vs. golden with black reticulation); and by foot webbing reaching to disks except toe IV (vs. reaching to disks on all toes) (see Blyth 1856; Poyarkov et al. 2014; Garg et al. 2019; our data).

For comparisons of *M. berdmorei* sensu stricto with other closely related members of the *M. berdmorei* species complex, see below.

Microhyla malcolmi Cochran, 1927

Figures 6C–D, 7B, 10B, 11, 12, 13; Tables 3, 6, S2

Suggested common name. Malcolm's narrow-mouthed frog.

Synonymy and chresonymy.

Microhyla malcolmi Cochran, 1927: 182. Holotype: USNM 72172 (Fig. 11). Type locality: "Pak Jong, Siam", now Pak Chong District, Nakhon Ratchasima Province, Thailand — Parker (1928: 473–499); Barbour and Loveridge (1929: 235); Bourret (1942: 509); Li et al. (2019: 568).

Microhyla fowleri Taylor, 1934: 284. Holotype: ANSP 19903 (Fig. 12). Type locality: "Chieng Mai, Siam", now Chiang Mai Province, Thailand — Dubois (1987: 3); Bourret (1942: 509); Taylor (1962: 560); Fei (1999: 292–293); Yang and Rao (2008: 124); Fei et al. (2009: 890–894); Fei et al. (2010: 481); Matsui (2011: 33–49); Matsui et al. (2011: 168, 171, 174, in part); Fei et al. (2012: 567); Poyarkov et al. (2014: 89–148); Pradana et al. (2017: 70–90); Li et al. (2019: 568).

Microhyla (Microhyla) fowleri — Dubois (1987: 3).

Microhyla berdmorei — Bourret (1942: 509, in part); Parker (1928: 473–499, in part); Barbour and Loveridge (1929: 235); Parker (1934: 127, in part); Taylor (1962: 560, in part); Heyer (1971: 64–66, in part); Berry (1975: 118–119, in part); Dubois (1987: 3, in part); Stuart (1999: 49, in part); Orlov et al. (2002: 99, in part); Ohler et al. (2002: 465–481, in part); Chan-ard (2003: 102, in part); Teynié et al. (2004: 35, in part); Nguyen et al. (2005: 44, in part); Stuart (2005: 35); Devi and Shamungou (2006: 317–324, in part); Grismer et al. (2006: 63, in part); Stuart and Emmett (2006: 6); Das and Yaakob (2007: 68, in part); Grismer and Aun (2008: 277, in part); Neang and Holden, (2008: 63, in part); Wogan et al. (2008: 88, in part); Chan et al. (2009: 278, in part); Nguyen et al. (2009: 97, in part); Chan-ard et al. (2011: 131, in part); Thong-aree et al. (2011: 99–106, in part); Grismer et

al. (2004: 18, in part); Manthey and Denzer (2014: 3–21, in part); Poyarkov et al. (2014: 89–148, in part); Sumarli et al. (2015: 8, in part); Vassilieva et al. (2016: 72–73, in part); Do et al. (2017: 88–89, in part); Mulcahy et al. (2018: 95, in part); Nguyen et al. (2019: 549–580, in part); Geissler et al. (2019: 40–63); Niyomwan et al. (2019: 222–223, in part); Garg et al. (2019: 15, in part); Poyarkov et al. (2020b: 136–163, in part); Gorin et al. (2020: 1–47, in part); Makchai et al. (2020: 116, in part); Poyarkov et al. (2021: 40, in part); Gorin et al. (2021: 97, in part); Zug (2022: 30, in part); Hoang et al. (2022: 35, in part); Frost (2024: page "*Microhyla berdmorei*" in part).

Holotype. USNM 72172 (adult female), by original designation (not physically examined by us, but see Fig. 11). Type locality: "Pak Jong, Siam", now Pak Chong District, Nakhon Ratchasima Province, Thailand (see Fig. 9).

Revised diagnosis. *Microhyla malcolmi* is characterized by the following combination of morphological attributes: (1) large body size (SVL 33.2–41.8 mm in males, 36.0–43.8 mm in females), with slender and triangular body habitus; (2) head longer than wide; (3) skin on dorsum slightly shagreened, laterally with sparse tiny tubercles; (4) snout obtusely pointed in dorsal, ventral, and lateral views; (5) first finger shorter than half of second finger length; (6) finger tips with weak disks lacking dorsomedial grooves; (7) toes with well-developed disks lacking or bearing rudimentary dorsomedial grooves; (8) tibiotarsal articulation of an adpressed limb extends far beyond snout; (9) toe webbing complete, reaching disks on all toes; webbing formula: 1I-1II1-1III1-1IV1-1V; (10) throat and chin dark-gray to almost black in males; belly bluish-gray anteriorly, yellowish posteriorly; (11) dorsal surfaces of fore- and hind limbs with wide dark crossbars, up to 3–4 crossbars on thighs; (12) brown patch above cloacal opening of variable shape and indistinct edges; (13) dark-brown dorsal "teddy-bear"-pattern distinct, usually edged with light-brown or beige anteriorly; (14) black spots and blotches of irregular shape on body flanks; (15) broad grayish-brown lateral band lateral stripe extending from armpit to groin; (16) light postocular stripe beige with black edging; (17) reddish spots on dorsum and dorsal surfaces of hindlimbs absent; (18) iris with black stripe below the pupil.

Material examined. In this study, we used morphological data from 52 specimens of *M. malcolmi* from Thailand, Laos, and Vietnam (see Table S2 for details).

Description of the specimen ZMMU A-7973 (Fig. 13).

An adult male specimen in a very good state of preservation. Body size large (SVL 37.1 mm; other measurements are presented in Table S2). Body habitus slender, triangular, dorsoventrally flattened (Fig. 13E). Head triangular in dorsal view; longer than wide (HW/HL ratio 0.94). Snout comparatively long and protruding (SL/HL ratio 0.34), obtusely pointed in dorsal view (Fig. 13A), gently obtusely pointed in profile, and noticeably extending beyond the edge of the lower jaw (Fig. 13E). Eyes large, protruding in dorsal and lateral views, significantly shorter than the snout (EL/SL ratio 0.75), and longer than the interorbital distance (IOD/EL ratio 0.88).

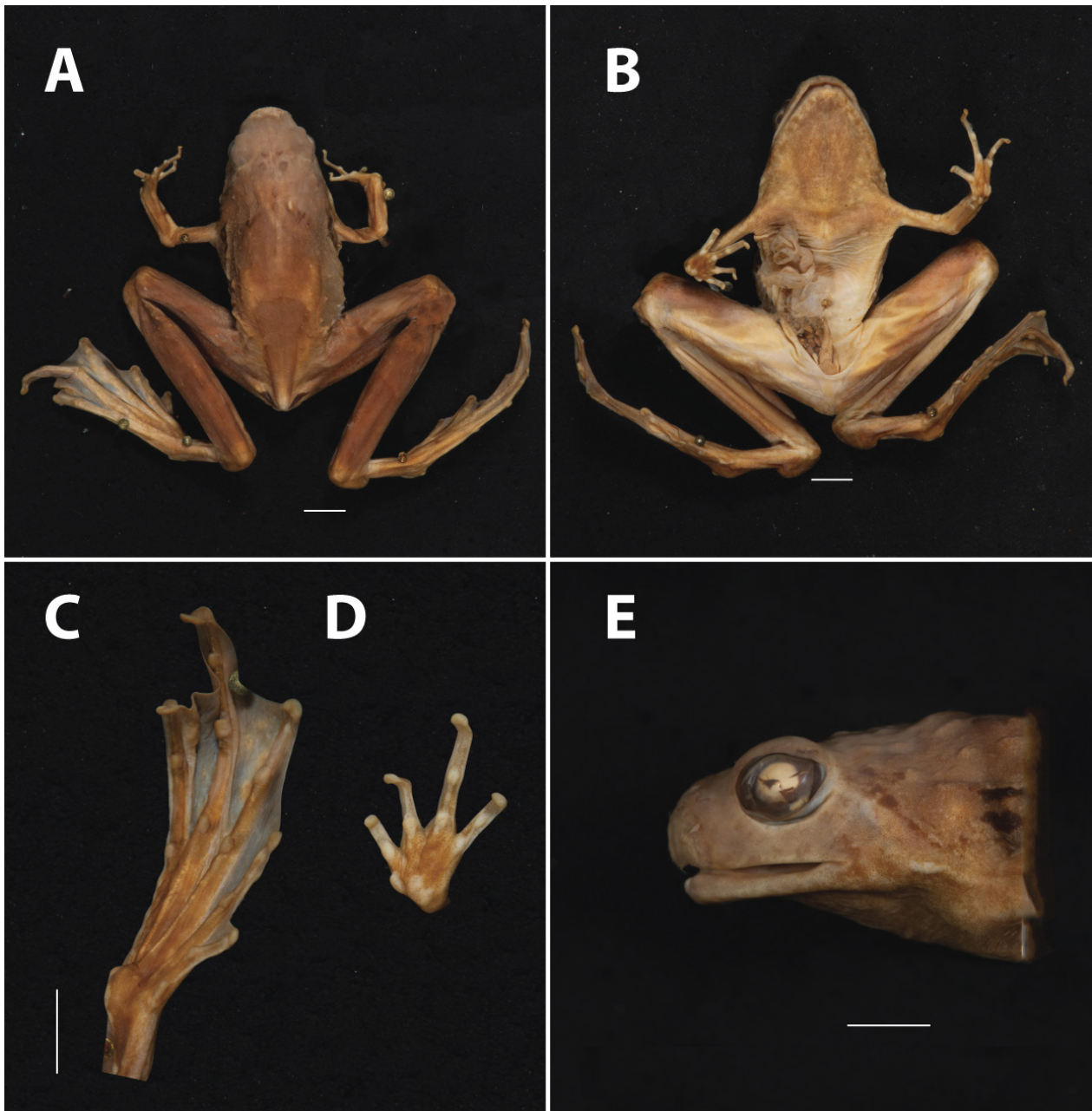


Figure 11. *Microhyla malcolmi* in preservative – specimen USNM 72172 (holotype, adult female) from Pak Chong, Nakhon Ratchasima Province, Thailand. **A** Dorsal aspect; **B** ventral aspect; **C** plantar view of the left foot; **D** volar view of the left hand; **E** lateral view of head. Scale bar equals 3 mm. Photographs by T. Hsu.

Canthus rostralis distinct, rounded; loreal area notably concave, smooth. Nostrils oval-shaped, with lateral orientation, located below the canthus rostralis; closer to eye than to the tip of snout. Interorbital distance broader than internarial distance (IND/IOD ratio 0.72). Upper eyelid smaller than interorbital distance (UEW/IOD ratio 0.69). Tympanum concealed, faintly developed glandular supratympanic fold extending from the posterior corner of eye to axilla (Fig. 13E). At the level of mouth corner, supratympanic fold bends posteriorly and extends to the forelimb insertion. Tongue slender, rounded, free behind for half of its length; vomerine teeth absent; gular vocal sac present, single.

Forelimbs short and slender (Fig. 13A); lower arm elongated and thin (LAL/FLL ratio 0.75), hand less than

half of forelimb length (HAL/FLL ratio 0.42). Fingers slender and elongated, webbing or skin fringes on fingers absent. First finger well-developed, subequal to half of the second finger length (Fig. 13D); the relative finger length formula: $I < II \leq IV < III$. Fingertips rounded, slightly expanded, noticeably narrower than the basal phalanges of the respective fingers. Finger tips lacking peripheral grooves, dorsomedial grooves absent, or present as a very shallow rudimentary medial notch (Fig. 6D). Finger tips almost uniform in width, with the tip of the first finger being slightly narrower. Subarticular tubercles on fingers distinct, large, rounded, and protruding, with the distal subarticular tubercle on the fourth finger being less distinct. Subarticular tubercle formula: 1, 1, 2, 2. Nuptial pad absent (Fig. 13D). Two metacarpal tubercles:

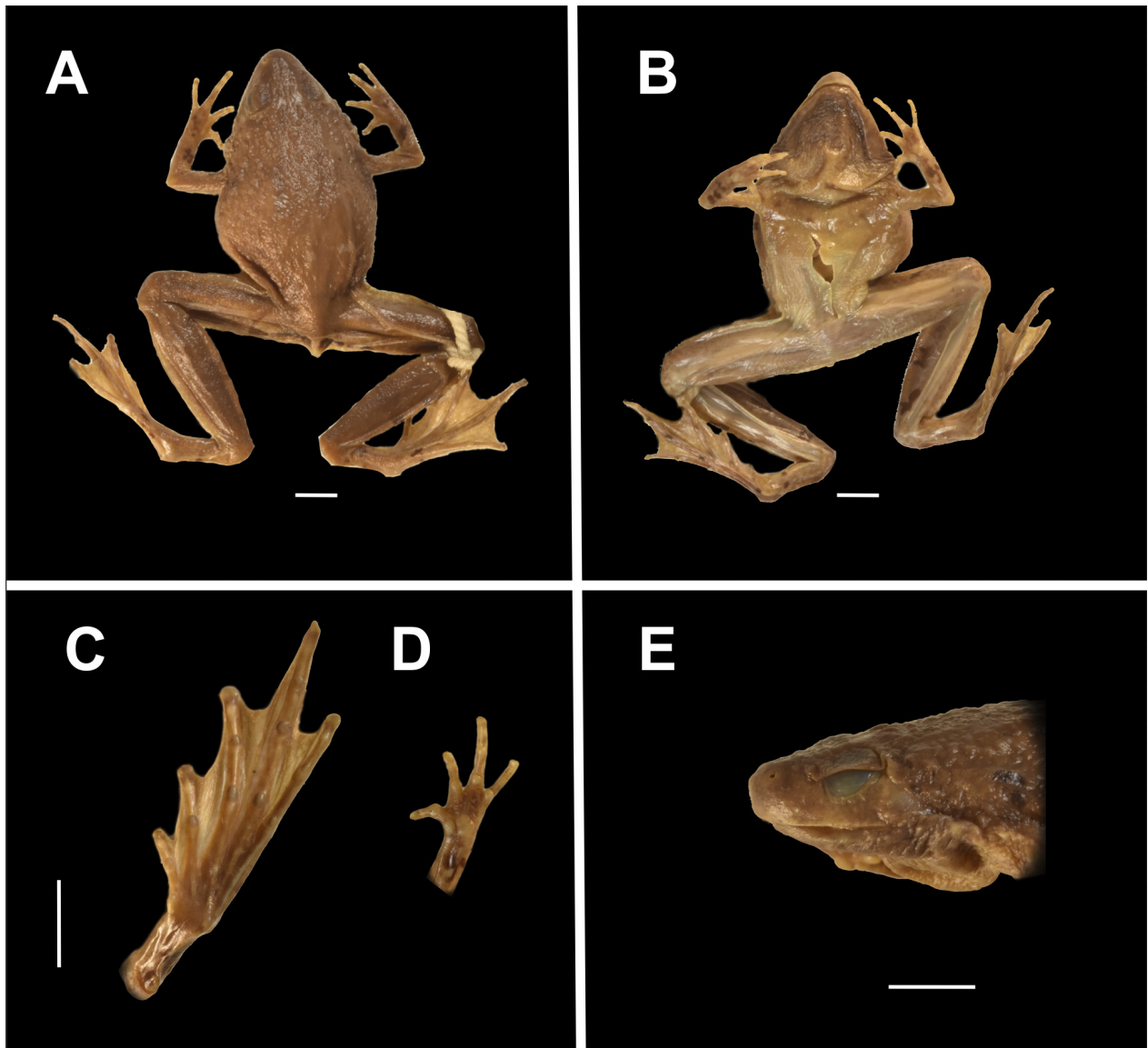


Figure 12. *Microhyla malcolmi* in preservative – specimen ANSP 19903 (holotype of *Microhyla fowleri* Taylor, 1934, adult female) from “Chieng Mai, Siam” (now Chiang Mai Province, Thailand). **A** Dorsal aspect; **B** ventral aspect; **C** plantar view of the left foot; **D** volar view of the left hand; **E** lateral view of head. Scale bar equals 3 mm. Photographs by N. Gilmore.

inner metacarpal tubercle distinct, protruding, rounded in shape; outer metacarpal tubercle rounded, flattened, its diameter equal to the diameter of inner metacarpal tubercle (OPTL/IPTL ratio 1.0).

Hindlimbs long and strong, slender, almost four times longer than the forelimbs (HLL/FLL ratio 3.66). Thighs robust and muscular (Fig. 13B), shanks elongated and slender, comprising approximately one-third of the hindlimb length (TL/HLL ratio 0.37). When the limbs are held at the right angle to the body, the heels significantly overlap. Tibiotarsal articulation of the addressed limb extends well beyond the tip of the snout. Foot length comprises more than one-third of the hindlimb length, being significantly shorter than tibia (FL/HLL ratio 0.27; TL/FL ratio 1.36). The relative toe lengths: $I < II < V \leq III < IV$. Shanks smooth, inner tarsal fold absent. Tips of all toes distinctly widened into small round disks wider than finger tips (4FDD/3FDD ratio 2.05). Dorsomedial longitudinal grooves absent on all toes or present as ru-

dimentary median notch at the medial edge of toe disk (Fig. 6C). The relative width of toes disks: $I < V < II < III \leq IV$. Toe webbing fully developed, web reaching disks on all toes; webbing formula: $i1-1ii1-1iii1-1iv1-1v$ (Fig. 6C). Subarticular tubercles on toes distinct, rounded, slightly protruding, subarticular tubercle formula: 1, 1, 2, 3, 2. Internal metatarsal tubercle of moderate size, oval, slightly elongated, with indistinct margins, less than half the length of the first toe (IMTL/1TOEL ratio 0.45). Outer metatarsal tubercle small but very distinct, rounded, prominent with well-defined margins, slightly longer than inner metatarsal tubercle (OMTL/IMTL ratio 1.12, Fig. 13C).

Skin texture is generally similar to that described for *M. berdmorei* (see above, Fig. 7A,B). Skin on dorsum slightly shagreened, with sparse small tubercles getting denser on the lateral sides of dorsum (Fig. 7B). Dorsal surfaces of forelimbs almost smooth, few tiny tubercles present on forearms. Dorsal surfaces of hindlimbs with

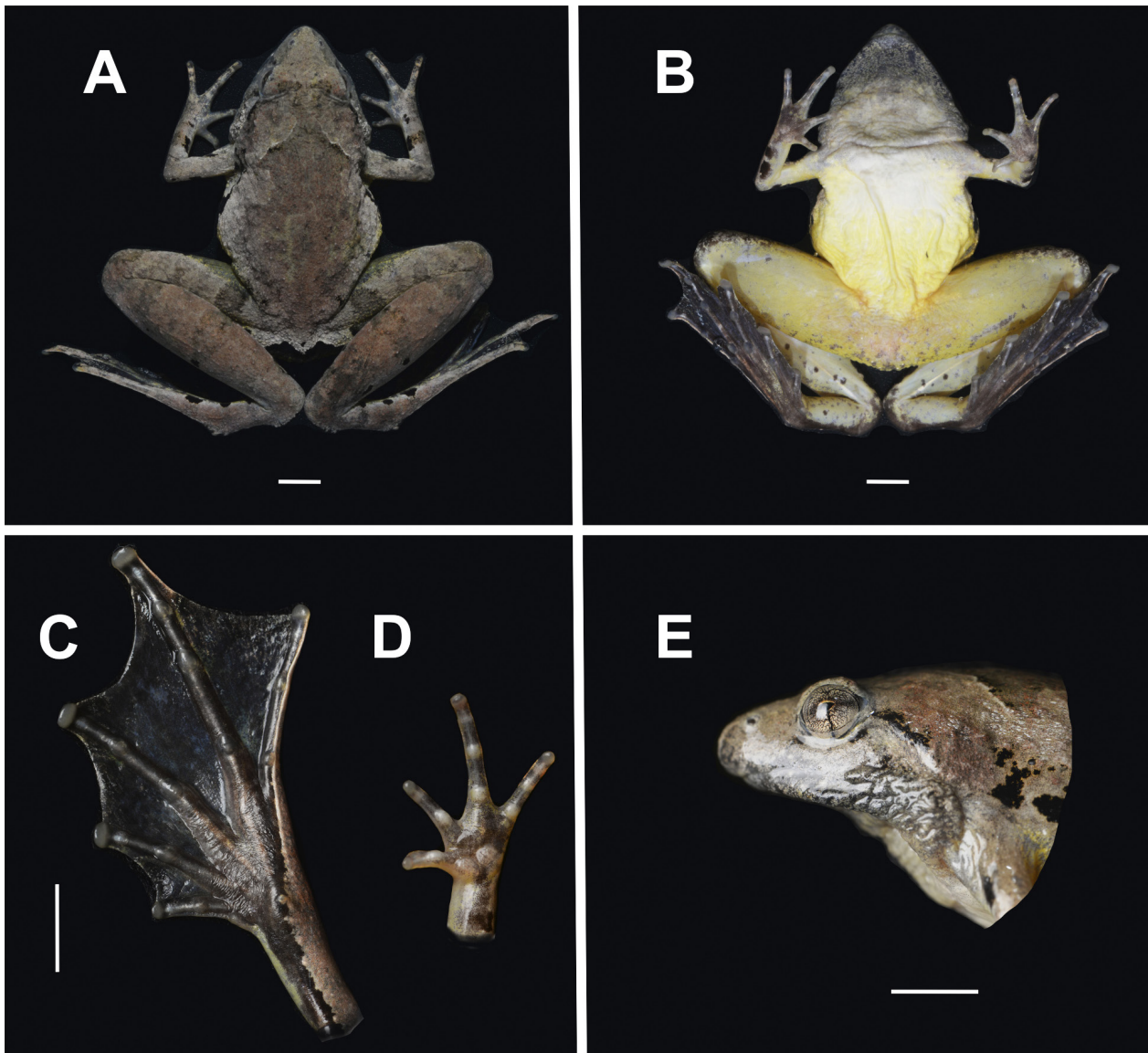


Figure 13. *Microhyla malcolmi* in preservative – ZMMU A-7973 (adult male) from Than To, Yala Province, Thailand. **A** Dorsal aspect; **B** ventral aspect; **C** plantar view of the left foot; **D** volar view of the left hand; **E** lateral view of head. Scale bar equals 3 mm. Photographs by N. A. Poyarkov.

sparse tubercles scattered across thighs and shanks; these tubercles are noticeably smaller than those on dorsum (Fig. 13A). Upper eyelid smooth. Body flanks smooth, numerous small warts present around the tympanal region. Ventral surfaces of body and limbs completely smooth (Fig. 13B). Cloacal opening unmodified, with posterior orientation.

Coloration in life. Dorsal background coloration gray-brown with a bronze tinge on the sides of the back, with a faint brown “teddy-bear” pattern medially (Fig. 7B). “Teddy-bear” marking with more distinct borders and beige edging anteriorly; the pattern becoming less distinct posteriorly, beige edging not discernible posteriorly. Interorbital dark bar incomplete, present as two indistinct dark-brown blotches between posterior parts of upper eyelids. Indistinct gray-brown marking in the shape of an inverted triangle between interorbital blotches and the “teddy-bear” pattern on dorsum (Fig. 13A). Posterior part

of dorsum brownish with indistinct gray blotches. A wide beige light postocular stripe running under the supratympanic fold from the posterior corner of eye to axilla, dorsally edged with black (Fig. 7B).

The lateral surfaces of the body and head slightly lighter than the dorsum. Snout, canthus rostralis and loreal area uniformly light olive-brown; dark-gray mottling present on the upper jaw; a few irregular black or brownish spots present below the eye. A broad grayish-brown band running from the posterior margin of the eye along the supratympanic fold. A narrow blackish-brown interrupted stripe running from the posterior corner of the eye to the axilla. A series of irregular black blotches and spots on body flanks between the axilla and groin. Except for the upper arm, limbs dorsally bearing indistinct dark-gray crossbars with indistinct edges; two crossbars visible on the lower arms; three crossbars present on each thigh and shank. Fingers and toes dorsally with narrow blackish transverse crossbars.

Belly lightly colored; anterior part of the belly bluish-gray, posterior portion of the belly, groin, ventral surfaces of upper arms, and thighs yellow to yellowish-gray with indistinct gray mottling on thighs (Fig. 7B). Gular area dark-gray; chin covered with dense gray mottling which gets darker at the edges of the mandible, mouth corners and gradually fades to bluish-gray towards the chest. Shanks ventrally light yellowish-gray, small black spots present on the ventral surfaces of the limbs. Fore- and hindlimbs ventrally grayish-yellow to yellowish. Ventral surfaces of hands (Fig. 13D) show no distinct pattern; feet ventrally with dark blackish-brown marking extending from the tibiotarsal joint to the ventral surfaces of toes and toe webbing (Fig. 13C). Iris bronze with black reticulations and a distinct black vertical stripe ventrally (Fig. 7B). Pupil round, black, outlined with a thin golden circle.

Coloration in preservative. After two years in preservative, the pattern described above generally remains unchanged, though light colors, like the yellowish coloration of the ventral surfaces and the olive-bronze coloration of dorsum faded to off-white and light gray, respectively. The dark dorsal pattern have become slightly less discernible. The characteristic dark spot above the cloacal opening, black spots and blotches on flanks, and dark markings on feet remain visible, they have turned dark grayish-brown. The limbs have turned yellowish-gray, and the dark crossbars still visible as indistinct dark-gray patterns. The ventral surfaces have faded to light beige; however, the dark markings on the chin have turned dark-gray but are still well discernible.

Variation. The examined individuals are overall quite similar in appearance. Differences in size and body proportions of the examined specimens are provided in Tables 4 and 5. In females, the body length (SVL) ranges from 33.1 to 43.8 mm ($n = 17$); in males, the SVL ranges 25.4–41.8 mm ($n = 35$). The dorsal background coloration varies from gray-brown to gray. Some male specimens demonstrate a darker and more contrasting dorsal “teddy-bear”-pattern (ZMMU A-5073, ZMMU A-4710). Breeding males have a darker-colored chin (dark-gray to blackish) than females (gray).

Etymology. The species was named after Dr. Malcolm Arthur Smith (1875–1958), a famous British herpetologist and physician, who collected many specimens in the early 20th century across Thailand, Vietnam and Malaysia. Recommended common names: “Malcolm’s narrow-mouthed frog” (English); “Nhái bầu Mao-com” (Vietnamese); “uzkorot Malkolma” (узкорот Малькольма, Russian); “Eung mae nao” (อีงแม่นาว, Thai).

Distribution. Based on our revalidation and definition of *M. malcolmi*, we define the range of this species as follows (Fig. 1): China (extreme south of Yunnan Province: Jinghong, Mengla, and Mengyang counties), Vietnam (northwestern, central, and southern parts of the country), Laos (entire country), Cambodia (entire country),

and Thailand (entire country). The southernmost record is known from Perlis State in Peninsular Malaysia (Fig. 1, locality 32). *Microhyla malcolmi* is also expected to occur in eastern Myanmar, though further studies are needed to clarify the extent of its distribution.

Natural history notes. *Microhyla malcolmi* inhabits various habitats, including primary and secondary forests as well as human-modified rural landscapes in lowland and hilly areas at elevations up to 2200 m a.s.l. In the lowland monsoon forests of southern Vietnam, this species appears to be associated with bamboo tangles (Vassilieva et al. 2016) and is also often recorded along forest streams. *Microhyla malcolmi* is active both day and night; according to Vassilieva et al. (2016), its diet consists mainly of ants. Breeding was observed in Vietnam and Cambodia and usually had two peaks of reproductive activity: in May-June and October-December (Neang and Holden 2008; Vassilieva et al. 2016). The noisy rasping call of breeding males can be heard at night from beside forest pools (Neang and Holden 2008). Breeding mainly takes place in slowly-flowing forest streams, ponds, rain pools, puddles and other similar still waterbodies; the reproductive activity usually starts after heavy rains. Clutches include hundreds of small (1.6–1.7 mm) pigmented floating eggs. In Thailand, the species prefers waterbodies with dead leaves and branches on silty bottoms for breeding (Meewattana 2022).

Tadpole. A detailed description of the larval morphology of *M. malcolmi* from Thailand was presented by Meewattana (2022) (referred to as *M. berdmorei* in his work). Tadpoles at late developmental stages reach 20–30 mm in length with large body, oval-shaped in dorsal view; interorbital distance ca. five times greater than internarial distance; mouth-snout distance equal to snout-eye distance; anal tube with vertical orientation reaching the edge of ventral fin; ventral tail fin less than twice as deep as dorsal tail fin; both fins deeper than tail musculature at the level of fourth proximal segment; tail tip tapering (Meewattana 2022). Oral disc terminal, comprising a half of interorbital distance in width; lacking papillae, jaw sheaths, or labial teeth (Meewattana 2022). In life, head, body, and caudal musculature pale grayish; posterior part of body dark-gray or black; dorsally with a weak dark marking between the eyes; tail fins transparent. Tadpoles of *M. malcolmi* are lentic suspension feeders.

Advertisement call. The male advertisement call of *M. malcolmi* represents a series of noisy rasping sounds that resemble the sound of a ratchet to the human ear. Heyer (1971) provided a brief description of an advertisement call for a *M. malcolmi* population from Sakaerat Experimental Station, Nakhon Ratchasima Prov., Thailand (referred to as *M. berdmorei* in his work). The duration of the call was 0.09–0.26 s, with each call consisting of 3–9 pulses at a pulse rate of 33–35 pulses per second, and the peak frequency of the call estimated at 1500–1800 Hz.

Our recording of *M. malcolmi* advertisement calls taken in Song Hinh Forest Reserve, Phu Yen Province,

Vietnam, included call series, each of them consisting of several calls (4–6; average 5.2 ± 1.4) emitted at a 2.3 ± 1.5 s (0.97 – 3.79 s) interval; a single call lasted for 0.22 ± 0.04 s (0.16 – 0.31) on average. Each call consisted of 9 ± 1.1 (8–10) pulses. The call's amplitude increased sharply, reached its peak in the first 0.05 – 0.10 s of call duration, and then gradually decreased towards the call's end; the last half of the call duration had a notably lower amplitude (491 ± 57 Hz) than the first half (Fig. 10B). We estimated the call peak frequency to be 1631 ± 93 Hz (1507 – 1809 Hz), which agrees well with the estimates of Heyer (1971).

Comparisons. *Microhyla malcolmi* was previously considered as a junior synonym of *M. berdmorei*, but this species can be differentiated from *M. berdmorei* sensu stricto by having: fully-developed foot webbing (I1–II1–1III1–1IV1–1V vs. I1–II1–2III1–2IV2–1V); supratympanic fold distinct (vs. indistinct); comparative shorter snout (SL/HL ratio 0.31 – 0.39 [avg. 0.34 , $n = 21$] in males, 0.32 – 0.37 [avg. 0.35 , $n = 9$] in females of *M. malcolmi* vs. 0.46 in male [$n = 1$], 0.45 – 0.46 [avg. 0.45 , $n = 3$] in females of *M. berdmorei* sensu stricto); snout shape in dorsal and ventral views (obtusely pointed vs. rounded); crossbars on thighs wide, 3–4 crossbars on each thigh (vs. crossbars narrow, up to 5–6 crossbars on each thigh); background color of dorsum grayish-brown (vs. olive-brown with a bronze tinge); head longer than wide (vs. head wider than long); finger tips with weak disks lacking dorsomedial grooves (vs. finger tips with weak disks bearing wide and shallow dorsomedial grooves); and toes with well-developed disks lacking or bearing rudimentary dorsomedial grooves (vs. toes with distinct disks, each bearing narrow and deep dorsomedial groove).

For comparisons of *M. malcolmi* with other members of the *M. berdmorei* species complex, see below.

Microhyla sunndaica sp. nov.

<https://zoobank.org/4D1D46BF-FED6-4A6C-8EE9-8017399D570E>

Figures 6E–F, 7C, 10C, 14, 15C–D; Tables 2, 3, 6

Suggested common name. Sundaic narrow-mouthed frog.

Chresonymy.

Microhyla berdmorei — Inger (1966: 149–151, in part); Grandison (1972: 59, in part); Dring (1979: 194, in part); Malkmus et al. (2002: 130–131, in part); Grismer et al. (2004: 18, in part); Das and Yaakob (2007: 68, in part); Grismer and Aun (2008: 277, in part); Chan et al. (2010: 203, in part); Teynić et al. (2010: 8); Matsui (2011: 35, 39); Matsui et al. (2011: 168, 171, 174, in part); Pradana et al. (2017: 70–90, in part); Firdaus et al. (2018: 1–6, in part); Haas et al. (2018: 89–114); Chan et al. (2019: 1057, in part); Nguyen et al. (2019: 549–580, in part); Gorin et al. (2020: 1–47, in part); Gorin et al. (2021: 97, in part); Poyarkov et al. (2021: 40, in part); Haas et al. (2022: 304–305); Badli-Sham et al. (2023: 49, 82, in part); Frost (2024: page “*Microhyla berdmorei*” in part).

Holotype. ZMMU A-8011, adult female from environs of Sungai Tua Recreational Forest, Selangor State, Malaysia (approximate coordinates: 3.32°N , 101.70°E), collected on January 27, 2003, by A. T. Aful.

Paratypes (n = 5). Two adult males: ZMMU A-8012 and ZMMU A-8014 and two adult females: ZMMU A-8010, ZMMU A-8013, all collection data are the same as for the holotype. One adult male: ZMMU A-6158 from Kuala Tahan District, Pahang State, Malaysia (approximate coordinates: 3.96°N , 102.44°E) collected on January 18, 2003, by A. T. Aful.

Diagnosis. *Microhyla sunndaica* sp. nov. is characterized by a combination of the following morphological features: (1) medium body size (27.5 – 27.9 mm in males, 28.3 – 31.4 mm in females), with moderately stocky and triangular body habitus; (2) head wider than long; (3) dorsal skin shagreened with numerous small tubercles; (4) snout pointed in dorsal and ventral views, bluntly rounded in lateral view; (5) first finger notably longer than half the length of second finger; (6) finger tips with well-developed disks bearing wide and deep dorsomedial grooves; (7) toes dilated in wide disks, each with complete and deep dorsomedial groove, separating the toe disk into a pair of scale-like pads; (8) tibiotarsal articulation of the adpressed limb extending far beyond the snout tip; (9) toe webbing reaching to the disks on all toes; webbing formula: I1–II1–2III1–1IV1–1V; (10) throat and chin dark-gray in males, beige in females; belly bright yellow in life; (11) dorsal surfaces of forelimbs without prominent crossbars, hindlimbs with 2–3 dark-brown crossbars on thighs and shanks; (12) two black blotches above cloacal opening edged with beige; (13) gray-brown dorsal “teddy-bear”-pattern distinct, edged with beige or white, anteriorly connecting with the dark interorbital bar; (13) dark spots and blotches on body flanks absent or scarce; (15) grayish lateral band with irregular edges extending from armpit to groin; (16) light postocular stripe absent; (17) reddish spots on dorsum and dorsal surfaces of hindlimbs absent; (18) iris uniform grayish-bronze, no black stripe below the pupil.

Description of the holotype (Fig. 14). An adult female specimen in a very good state of preservation. Body size medium (SVL 31.4 mm; other measurements are presented in Table 2). Body habitus stocky, triangular, and significantly dorsoventrally flattened (Fig. 14E). Head triangular in dorsal view; wider than long (HW/HL ratio 1.16). Snout comparatively short and protruding (SL/HL ratio 0.45), appearing pointed in dorsal and ventral views (Fig. 14E), smoothly rounded in profile, and slightly extending beyond the edge of the lower jaw (Fig. 14E). Eyes comparatively small, slightly protruding in lateral view, not protruding in dorsal view, significantly shorter than the snout (EL/SL ratio 0.76), and slightly shorter than the interorbital distance (IOD/EL ratio 1.03). Canthus rostralis distinct, rounded; loreal area slightly concave. Nostrils oval-shaped, with dorso-lateral orientation, situated almost on the canthus rostralis, closer to tip of snout than to eye. Interorbital distance broader than

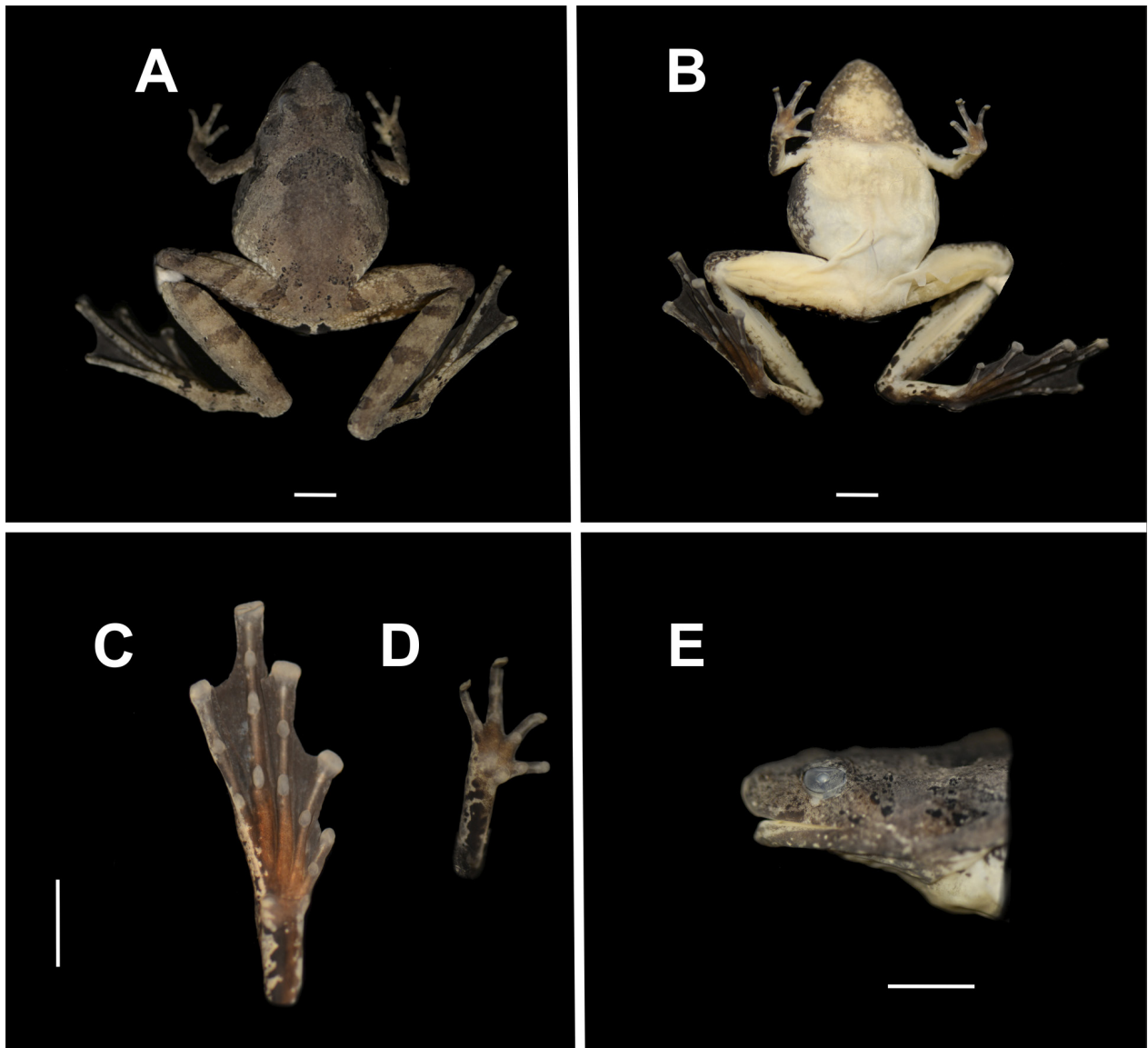


Figure 14. *Microhyla sundaica* sp. nov. in preservative – ZMMU A-8011 (holotype, adult male) from environs of Sungai Tua Recreational Forest, Selangor State, Malaysia: **A** Dorsal aspect; **B** ventral aspect; **C** plantar view of the right foot; **D** volar view of the left hand; **E** lateral view of head. Scale bar equals 3 mm. Photographs by A. V. Trofimets.

the internarial distance (IND/IOD ratio 0.77). Upper eyelid length narrower than the interorbital distance (UEW/IOD ratio 0.66). Tympanum concealed, supratympanic fold absent (Fig. 14E). Tongue slender, rounded, free for the posterior four-fifths of its length; vomerine teeth absent. Eggs seen through the incision on the left lateral side of belly small, rounded, ca. 1.0–1.1 mm in diameter, pigmented.

Forelimbs short and slender (Fig. 14A); lower arm elongated and thin (LAL/FLL ratio 0.83), hand less than half of forelimb length (HAL/FLL ratio 0.47). Fingers slender and elongated, webbing or skin fringes on fingers absent. First finger well-developed, notably longer than half of the second finger length (Fig. 14D); the relative finger lengths as follows: $I < II < IV < III$. Fingertips rounded, expanded into well-developed disks narrower than the basal phalanges of the respective fingers. Finger tips with peripheral grooves, dorsally with a wide and deep dorsomedial notch (Fig. 6F). Finger tips almost

equal in width, with the first fingertip slightly narrower. Subarticular tubercles on fingers distinct, large, rounded, and protruding; edges of the distal subarticular tubercle on the fourth finger less distinct. Subarticular tubercle formula: 1, 1, 2, 2 (Fig. 14D). Two metacarpal tubercles: inner metacarpal tubercle distinct, protruding, rounded in shape; outer metacarpal tubercle rounded, flattened, its diameter much less than the diameter of inner metacarpal tubercle (OPTL/IPTL ratio 1.40).

Hindlimbs long, slender, almost four times longer than the forelimbs (HLL/FLL ratio 3.96). Thighs robust and muscular (Fig. 14B), shanks notably elongated and slender, comprising approximately one-third the length of the hindlimb (TL/HLL ratio 0.35). When the limbs are held the right angle to the body, the heels significantly overlap. Tibiotarsal articulation of the adpressed limb extends well beyond the tip of the snout. The foot length is more than one-third of the hindlimb length and significantly shorter than shanks (FL/HLL ratio 0.29; TL/

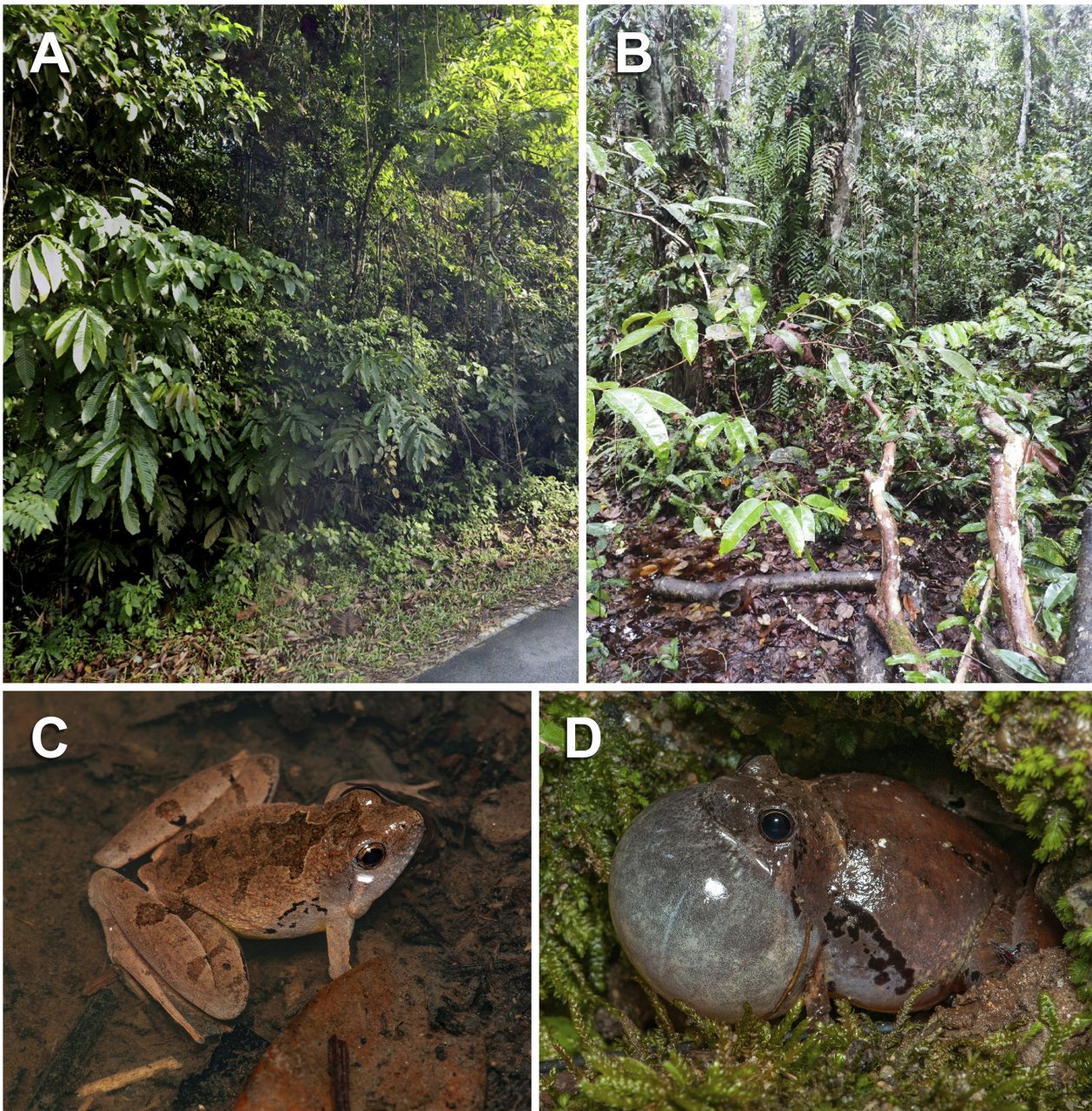


Figure 15. Natural habitat of *Microhyla sundaica* sp. nov. at the type locality in Sungai Tua, Selangor State, Peninsular Malaysia (A), and in Gunung Jerai Mt., Kedah State, Peninsular Malaysia (B); calling males of *M. sundaica* sp. nov. from Sedim, Kedah State, Peninsular Malaysia in situ (C, D) (not collected). Photographs by M. A. Muin.

FL ratio 1.21). The relative toe lengths as follows: $I < II < V \leq III < IV$. Shanks smooth, with the inner tarsal fold absent. The tips of all toes distinctly widened into wide heart-shaped disks, almost twice as wide as finger disks (4TDD/3FDD ratio 1.77). Toe webbing fully developed, reaching the disks of all toes; webbing formula: 11-1111-2111-1111-11 (Figs 6E, 14C). Toe subarticular tubercles distinct, rounded, slightly protruding, subarticular tubercle formula: 1, 1, 2, 3, 2. The internal metatarsal tubercle of moderate size, oval, slightly elongated, with indistinct margins, less than half the length of the first toe (IMTL/1TOEL ratio 0.31). Outer metatarsal tubercle small but distinct, rounded, prominent with well-defined margins, slightly larger than the inner metatarsal tubercle (OMTL/IMTL ratio 1.45).

Skin on the dorsum slightly tuberculated with numerous small tubercles covering both the middle and the lateral parts of the dorsum (Fig. 7C). Dorsal surfaces of forelimbs smooth. Dorsal surface of hindlimbs with numerous sparse tubercles scattered across thighs and shanks; the tubercles on the hindlimbs notably smaller than those on dorsum (Fig. 14A). Upper eyelid smooth. Body flanks smooth. Numerous small warts present around the tympanal region. Ventral surfaces of body and limbs smooth (Fig. 14B). Cloacal opening unmodified, directed posteriorly.

Coloration in life. The dorsal background coloration in life was gray-bronze with a light-gray tint on the sides of the dorsum, with a faint gray-brown “teddy-bear”-pat-

tern in the middle of the dorsum (Fig. 7C). The “teddy-bear”-pattern has regular light edging, which becomes less distinct posteriorly. A pronounced gray-brown inter-orbital band in the shape of an inverted triangle with irregular borders runs across the head between the posterior parts of the upper eyelids, and is posteriorly connected with the “teddy-bear”-pattern on the dorsum. The lateral sides of the dorsum are lighter and have a light grayish-brown tint. A pair of black spots, edged with beige, located above the cloacal opening.

Body flanks and head lateral sides slightly lighter than the dorsum. Bronze blotches on both sides of the head on canthus rostralis; snout uniformly dark olive-brown. Upper jaw bronze-brown with a few irregular gray or white spots below the eye. Light postocular stripe or other markings in tympanal area or around axilla absent. On forelimbs, no conspicuous stripes or spots; two grayish-brown crossbars with indistinct border present on thighs and shanks. Dorsal surfaces of fingers and toes uniformly gray, lacking transverse stripes or dark spots.

Belly and chest bright yellow, with a few irregular grayish spots on throat and chin, covered with sparse dark-gray spotting (Fig. 7C). This coloration becomes notably darker along the edges of the mandible and the mouth corners. Ventral surfaces of the limbs yellow to grayish-yellow with rare gray spots and mottling. Ventral surfaces of arms (Fig. 14D) and feet (Fig. 14C) with irregular brownish-black blotches. Iris light grayish-bronze without dark reticulations and lacking the dark vertical stripe below the pupil. Pupil round, black, outlined with a thin bronze circle.

Coloration in preservative. After 21 years in preservative, the pattern described above generally remained unchanged, but bright yellow and light-brown colors faded to off-white and gray. The dorsal pattern became less prominent, but all the dark markings on dorsum remain discernible. The dark transverse crossbands and spots on fore- and hindlimbs became less distinct. The gray markings on the chin were still visible as faint gray mottling.

Variation. The examined members of the type series are overall quite similar in appearance. Differences in size and body proportions are presented in Tables 4 and 5. We observed sexual differences in body length, with males (SVL 27.5–27.9 mm, $n = 3$) having significantly smaller SVL than females (SVL 28.3–31.4 mm, $n = 3$). No differences in coloration between males and females were observed except for the darker coloration of throat and chin in males; the dorsal coloration varies from gray-bronze to light-brown. The dorsal “teddy-bear”-pattern has a darker coloration; in some individuals (ZMMU A-8012 and ZMMU A-8014), the dorsal pattern was more contrasting and had more clear edges. In other individuals, the dorsal pattern was duller with less distinct borders. Two females (ZMMU A-8010 and ZMMU A-8013) had somewhat brighter light-brown coloration of the hindlimbs different from that of the dorsum. In all examined individuals, there were no signs of the presence of a vertical brown stripe on iris except ZMMU A-6158, which showed a ru-

dimentary dark stripe below the pupil that did not reach the ventral edge of the iris.

Etymology. The species epithet “*sundaica*” is a latinized adjective in nominative singular, adjusted to the feminine gender of the genus name “*Microhyla*”, and is given in reference to the distribution of the new species, which inhabits the three major landmasses of the Sundaland, or Sundaic Region, namely: Peninsular Malaysia, Sumatra, and Borneo. “Sundaica” is the Latin name for Sundaland. Recommended common names: “Sundaic narrow-mouthed frog” (English); “Nhái bầu Sunda” (Vietnamese); “Zondskiy uzkorot” (Зондский узкорот, Russian); “Eung mae nao Malayu” (อึ่งแมหนาวมาลายู, Thai); “Katak mulut sempit Sunda” (Malay).

Distribution. According to our data, *M. sundaica sp. nov.* inhabits Malaysia (the continental part of the country, and Sabah State on the island of Borneo), Indonesia (on the islands of Borneo (South Kalimantan Province) and Sumatra (Bengkulu and Sumatera Selatan provinces) (Fig. 1). It is likely that the actual distribution of *M. sundaica sp. nov.* is wider, and it can be found in other parts of Sundaland, including Sarawak State of Malaysia, and other provinces of Sumatra. Despite our repeated efforts, we failed to record *M. sundaica sp. nov.* in southern Thailand, though the possibility that this species occurs in the southernmost provinces of the country (Narathiwat and Yala provinces) cannot be ruled out completely.

Natural history notes. The new species is often recorded while calling from the banks or in shallow rain puddles or swamps (Fig. 15A–B). Although most of the *M. sundaica sp. nov.* records came from recreational forest areas, this species is also likely to inhabit pristine forests, being especially abundant along the streams or near shallow intermittent pools. Inger et al. (2017) reported that in Borneo male individuals of this species (which he referred to as *M. berdmorei*) were encountered during vocalization activity while they were hiding in burrows or under dead leaves in the leaf litter; usually males call from ca. 1–5 meters from waterpools or stream banks. In Borneo, this species prefers stagnant temporary waterbodies for reproduction (Inger et al. 2017). *Microhyla sundaica sp. nov.* has mostly crepuscular activity and is often observed at night actively foraging after heavy rains, usually from 19:00 to 23:00 h. The diet and predators of the new species remain unknown. At the type locality in environs of Sungai Tua Recreational Forest, Selangor State, Malaysia (Fig. 15A), *M. sundaica sp. nov.* was recorded in sympatry with *Ingerophrynus parvus* (Boulenger, 1887), *Kalophrynus kiewi* Matsui, Eto, Belabut & Nishikawa, 2017 and *M. butleri* Boulenger, 1900. Inger et al. (2017) noted that the new species occurs in mature and secondary forests, mostly at low elevations. Sumarli et al. (2015) reported that male specimens of this species were recorded at night while calling from the top of a boulder at the water’s edge within small puddles; while some specimens were found sitting on mud or in flooded ruts, most were hiding in vegetation along the forest trails. In Peninsu-

lar Malaysia, the new species was recorded in sympatry with *M. heymonsi* Vogt, 1911, and with *M. butleri* (Sumarli et al. 2015). Dring (1979) reported that in Borneo, *M. sundaica* **sp. nov.** males were calling in one chorus with *M. borneensis* Parker, 1928. In Selangor and Kedah State, Peninsular Malaysia, the species prefers temporary, stagnant pools of water for breeding, with rich leaf litter around (Leong 2004; our observations); males usually call from small holes in the ground on the bank ca. 15–25 cm from the wateredge, or while floating on the water surface (Fig. 15C–D).

Tadpole. A detailed description of the larval morphology of *M. sundaica* **sp. nov.** from Selangor, Peninsular Malaysia, was presented by Leong (2004); additional information was provided by Haas et al. (2022). Tadpole total length not exceeding 23 mm. At late development stages, body large, elliptical in dorsal view, body length comprises 162%–168% of body width; dorsum flattened; venter rounded; at Gosner stage 37, body length comprises 39% of total length; snout rounded in dorsal and lateral views; eyes with lateral orientation; nostril located closer to snout tip than to eye; interorbital distance ca. five times greater than internarial distance; spiracle medial with a smooth convex margin, located on ventral surface; spiracle–snout distance comprises 83%–88% of body length; vent tube opening medial, directed ventrally, continuous with ventral fin; ventral tail fin deeper than dorsal tail fin for proximal half; tail gradually tapering towards a narrowly pointed tip lacking terminal filament. Oral disc terminal, lacking papillae or keratinized structures; lower labium not expanded, with distinct median ‘U’-shaped arch. In life, dorsal and lateral surfaces of head and body yellowish; body wall translucent, and caudal musculature whitish; posterior parts of body darker; tail fins clear or have very light pigmentation (Leong 2004). Tadpoles of *M. sundaica* **sp. nov.** are lentic suspension feeders.

Advertisement call. We recorded the advertisement call of the new species in Gunung Jerai Mt., Kedah, Peninsular Malaysia. The male advertisement call of *M. sundaica* **sp. nov.** consists of a series of short nasal rasping squeaks. Each call series consisted of usually seven calls (6–8) emitted at a 1.8 ± 0.3 s (1.34–2.30 s) interval; a single call series lasted for 3.8 ± 2.3 s (2.5–6.7). Individual calls lasted for 0.16 ± 0.03 s (0.12–0.21), and each call consisted of 13 ± 2.3 (8–16) pulses. Each call consisted of two syllables: the introductory note and the main call; the frequency of the introductory note was much lower (739 ± 112 Hz) than that of the main call; the relative amplitude sharply increased in the middle of the call, reaching its maximum in the second half of its duration, and then slowly decreased towards the call end (Fig. 10C). The call’s peak frequency was 2029 ± 106 Hz (1898–2203 Hz).

Comparisons. We here compare *M. sundaica* **sp. nov.** with the six other species of the *M. berdmorei* group species (*M. berdmorei* sensu stricto, *M. malcolmi*, *M. peninsularis* **sp. nov.** (described below), *M. darevskii*, *M. picta*, and *Mi. pulchra*). The main diagnostic characters separat-

ing the new species from these congeners are summarized in Table 5.

Microhyla sundaica **sp. nov.** is distinguished from *M. berdmorei* sensu stricto by having: smaller body size in both sexes (SVL 27.5–27.9 mm in males, 28.3–31.4 mm in females vs. 33.0 mm in male, 36.3–38.1 mm in females); finger I length greater than half of finger II length ($F1 > \frac{1}{2}F2$ vs. $F1 < \frac{1}{2}F2$); body habitus stocky (vs. slender); toe webbing complete, webbing formula: $I1-1II1-2III1-1IV1-1V$ (vs. webbing formula: $I1-1II1-2III1-2IV2-1V$); dorsomedial grooves on finger and toe disks present (vs. weak or rudimentary); snout in lateral profile bluntly rounded (vs. obtusely pointed); dorsal color gray-bronze with a grayish tint (vs. olive-brown); interorbital markings gray-brown (vs. dark-brown or black); limbs lacking transverse dark crossbars (vs. up to 5–6 narrow prominent crossbars on thighs); iris coloration gray-bronze lacking reticulation and dark vertical stripe (vs. bronze with a black reticulation and a dark vertical stripe below the pupil).

Microhyla sundaica **sp. nov.** is further distinguished from *M. malcolmi* by having: small body size in both sexes (SVL 27.5–27.9 mm in males, 28.3–31.4 mm in females vs. 33.2–41.8 mm in males, 36.0–43.8 mm in females); body habitus stocky (vs. slender); finger I length greater than half of finger II length ($F1 > \frac{1}{2}F2$ vs. $F1 < \frac{1}{2}F2$); snout in lateral profile rounded (vs. obtusely pointed); dorsomedial grooves on finger and toe disks present (vs. absent); dorsal color gray-bronze with a grayish tint (vs. gray-brown); limbs with faint gray spots or stripes lacking transverse crossbars (vs. up to 3–4 dark transverse crossbars); iris coloration gray-bronze lacking reticulation and dark vertical stripe (vs. bronze with a black reticulation and a dark vertical stripe below the pupil).

Microhyla sundaica **sp. nov.** is distinguished from *M. darevskii* by having: finger disks present (vs. absent); dorsomedial grooves on toe disks present (vs. absent); slightly less developed foot webbing ($I1-1II1-2III1-1IV1-1V$ vs. $I1-1II1-1III1-1IV1-1V$); dorsal color gray-bronze with grayish tint (vs. brown); interorbital markings gray-brown blotches (vs. dark-brown band); belly color in life bright yellow with irregular grayish spots (vs. no yellow color on belly); limbs with faint gray spots or stripes (vs. absent); iris coloration gray-bronze without reticulation (vs. golden with a black reticulation).

Microhyla sundaica **sp. nov.** further differs from *M. picta* by having: body habitus stocky (vs. stout); dorsum slightly tuberculated with small tubercles (vs. strongly tubercular with large warts); finger I length greater than half of finger II length ($F1 > \frac{1}{2}F2$ vs. $F1 < \frac{1}{2}F2$); finger disks present (vs. absent); toe disks present (vs. absent); dorsomedial grooves on toe disks present (vs. absent); tibiotarsal articulation of an addressed limb reaching well beyond snout (vs. eye level); better development of foot webbing ($I1-1II1-2III1-1IV1-1V$ vs. $I2-2\frac{3}{4}III2\frac{3}{4}-2\frac{3}{4}III2\frac{3}{4}-3\frac{3}{4}IV4-2\frac{1}{2}V$); dorsal color gray-bronze with grayish tint (vs. brown to sandy); interorbital markings gray-brown blotches (vs. dark-brown band); belly color bright yellow with irregular grayish spots (vs. no yellow color on belly); limbs with faint gray spots or stripes (vs.

brown transverse crossbars); iris coloration gray-bronze without reticulation (vs. golden with a black reticulation and with a distinct vertical dark stripe).

Microhyla sundaica **sp. nov.** can be further differentiated from *M. pulchra* by having: skin on dorsum shagreened with numerous small tubercles (vs. completely smooth); finger I length greater than half of finger II length ($F1 > \frac{1}{2}F2$ vs. $F1 < \frac{1}{2}F2$); finger disks present (vs. absent); toe disks present (vs. absent); dorsomedial grooves on toe disks present (vs. absent); tibiotarsal articulation of an adpressed limb reaching well beyond snout (vs. to snout or just beyond); better developed foot webbing (I1-III1-2III1-IV1-1V vs. I1½-2III1-3III2-3¼IV3½-2V); dorsal color gray-bronze with grayish tint (vs. characteristic agate pattern consisting of numerous light and dark brown lines); interorbital markings as gray-brown blotches (vs. brown transverse band); limbs with faint gray spots or stripes (vs. dark-brown to olive-brown transverse crossbars); iris coloration gray-bronze without reticulation (vs. gray with black reticulation and with a distinct vertical dark stripe).

For comparisons of the new species with *M. peninsularis* **sp. nov.**, see below.

Microhyla peninsularis **sp. nov.**

<https://zoobank.org/31BB3D43-22A7-44C1-AF02-68DF9B-C0A564>

Figures 6G, H, 7D, 16; Tables 2, 3, 6

Suggested common name. Peninsular narrow-mouthed frog.

Chresonymy.

Microhyla berdmorei — Berry (1975: 118–119, in part); Dring (1979: 194, in part); Manthey and Grossmann (1997: 60, in part); Das and Yaakob (2007: 68, in part); Grismer and Aun (2008: 277, in part); Chan et al. (2010: 203, in part); Matsui et al. (2011: 168, 171, 174, in part); Thong-aree et al. (2011: 99–106, in part); Sumarli et al. (2015: 8, in part); Firdaus et al. (2018: 1–6, in part); Nguyen et al. (2019: 549–580, in part); Niyomwan et al. (2019: 222–223, in part); Gorin et al. (2020: 1–47, in part); Makchai et al. (2020: 116, in part); Eprilurahman et al. (2021: 456); Gorin et al. (2021: 97, in part); Poyarkov et al. (2021: 40, in part); Frost (2024, page “*Microhyla berdmorei*” in part).

Holotype. ZMMU A-8016 (field number NAP-12747), an adult female from the Lam Plok Waterfall, Trang Province, Thailand (7.584°N, 99.799°E; elevation 200 m a.s.l.), collected on August 20, 2022, by

Paratypes (n = 3). One adult female ZMMU A-8015 (field number NAP-12746), with collection data the same as for the holotype. Two adult males, ZMMU A-8017 (field number NAP-13182) and ZMMU A-8018 (field number NAP-13183), from Namtok Khao Chong, Trang Province, Thailand (7.649°N, 99.739°E; elevation 92 m a.s.l.) collected on August 24, 2021, by P. Pawangkhanant.

Diagnosis. *Microhyla peninsularis* **sp. nov.** is characterized by the following combination of morphological features: (1) medium body size (SVL 22.1–22.2 mm in males, 30.9–33.2 mm in females), with moderately stocky and triangular body habitus; (2) head wider than long; (2) dorsal skin almost smooth; (3) snout short and bluntly rounded in dorsal, ventral, and lateral views; (4) first finger longer than half of the length of second finger; (5) finger tips weakly expanded into small disks with wide and deep dorsomedial grooves; (6) toes with distinct disks, each with wide and shallow dorsomedial groove separating the disk into a pair of scale-like pads; (7) tibiotarsal articulation of an adpressed limb extending far beyond the snout tip; (8) toe webbing reaching toe disks on all toes except the fourth and third toes; webbing formula: I1-1II1-2III1-1IV2-1V; (9) throat and chin gray in females, with dark-gray mottling in males; belly in life yellowish-white lacking dark markings; (10) dorsal surfaces of forelimbs without prominent dark crossbars, hindlimbs with 1–3 weak and indistinct brownish crossbars; (11) two dark-brown blotches above cloacal opening; (12) dorsum rusty-bronze with indistinct darker “teddy-bear”-pattern lacking clear borders and light edging; (13) dark spots and blotches on body flanks absent or scarce; (14) grayish-bronze lateral band with irregular edges extending from armpit to groin; (16) light postocular stripe absent; (17) reddish spots on dorsum and dorsal surfaces of hindlimbs absent; (18) iris with short black stripe below the pupil.

Description of the holotype (Fig. 16). An adult male specimen in a very good state of preservation. Body size medium (SVL 30.9 mm; other measurements are presented in Table 2). Body habitus stocky, triangular, and slightly dorsoventrally flattened (Figs 7D, 16E). Head short, triangular in dorsal view; wider than long (HW/HL ratio 1.23). Snout very short (SL/HL ratio 0.43) and slightly protruding, bluntly rounded in dorsal and ventral views (Fig. 16A,B), bluntly rounded in profile, and only slightly extending beyond the edge of the lower jaw (Fig. 16E). Eyes comparatively small, slightly protruding in lateral view, not protruding in dorsal view (Fig. 16A), eye length subequal to snout length (EL/SL ratio 0.99), and significantly larger than interorbital distance (IOD/EL ratio 0.74). Canthus rostralis indistinct; loreal area slightly concave. Nostrils oval-shaped, with lateral orientation, located closer to tip of snout than to eye. Interorbital distance slightly wider than internarial distance (IND/IOD ratio 0.95). Upper eyelid length less than interorbital distance (UEW/IOD ratio 0.86). Tympanum concealed, supratympanic fold indistinct (Fig. 16E). Tongue slender, rounded, free for the posterior four-fifths of its length; vomerine teeth absent.

Forelimbs short and slender (Fig. 16A); lower arm elongated and thin (LAL/FLL 0.79), hand less than half of forelimb length (HAL/FLL 0.46). Fingers slender and elongated, webbing or skin fringes on fingers absent. First finger well-developed, notably longer than half of the second finger length (Fig. 16D); the relative finger lengths as follows: $I < II < IV < III$. Fingertips rounded, weakly expanded into small disks, noticeably narrower than the basal phalanges of the respective fingers. Finger

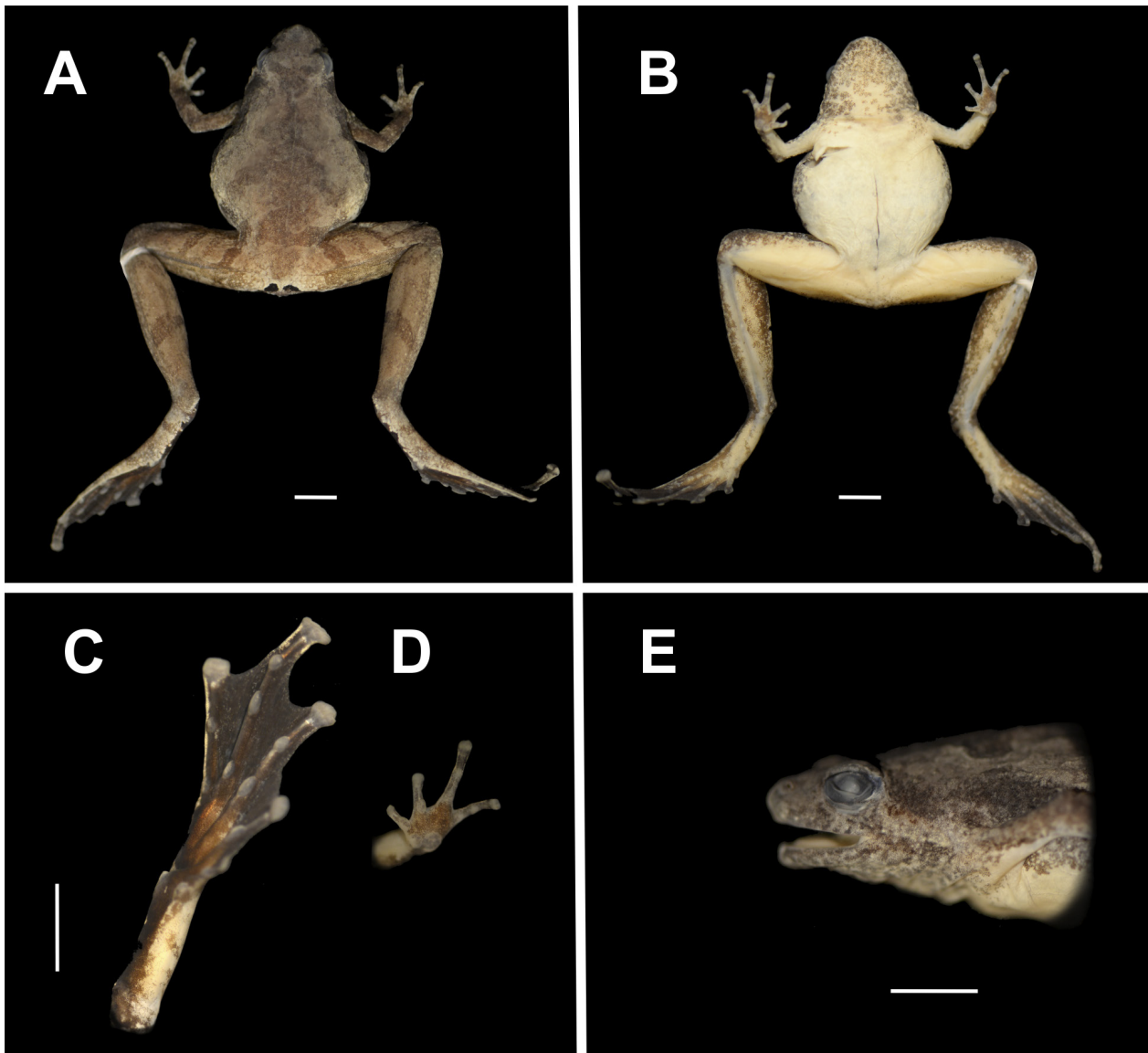


Figure 16. *Microhylya peninsularis* sp. nov. in preservative – Specimen ZMMU A-8016 (holotype, adult female) from Lam Plok Waterfall, Trang Province, Thailand: **A** Dorsal aspect; **B** ventral aspect; **C** plantar view of the right foot; **D** volar view of the left hand; **E** lateral view of head. Scale bar equals 3 mm. Photographs by A. V. Trofimets.

tips with peripheral grooves and a wide and deep dorso-medial notch present on the dorsal surface of each finger disk (Fig. 6H). Finger disks almost equal in width, with the first finger disk being slightly narrower. Subarticular tubercles on fingers distinct, large, rounded, and protruding; edges of the distal subarticular tubercle on the fourth finger less distinct. The subarticular tubercle formula: 1, 1, 2, 2; nuptial pad absent (Fig. 16D). Two metacarpal tubercles: inner metacarpal tubercle distinct, protruding, rounded in shape; outer metacarpal tubercle rounded, flattened, its diameter slightly exceeding the diameter of inner metacarpal tubercle (OPTL/IPTL ratio 1.18).

Hindlimbs long, slender, almost four times longer than forelimbs (HLL/FLL ratio 4.21). Thighs robust and muscular (Fig. 16B), shanks moderately elongated and slender, comprising approximately one-third the length of the hindlimb (TL/HLL ratio 0.36). When the limbs are held at the right angle to the body, the heels significantly overlap. Tibiotarsal articulation of the adpressed limb

extends well beyond the tip of the snout. Foot length comprises more than one-third of the hindlimb length (FL/HLL ratio 0.23), being significantly shorter than the tibia (TL/FL ratio 1.34). The relative toe lengths as follows: $I < II < V \leq III < IV$. Shanks smooth, inner tarsal fold absent. Tips of all toes distinctly widened into oval-shaped disks, toe disks twice as wide as finger disks (4FDD/3FDD ratio 1.97) and the proximal phalanges of respective toes. Toes webbing complete fully developed, reaching toe disks on all toes except fourth and third toes; webbing formula: $11-1111-2111-11v2-1v$ (Figs 6G, 16C). Toe subarticular tubercles distinct, rounded, slightly protruding, subarticular tubercle formula: 1, 1, 2, 3, 2. The internal metatarsal tubercle oval, slightly elongated, with indistinct margins, comprising less than half the length of the first toe (IMTL/1TOEL ratio 0.32). The outer metatarsal tubercle small but distinct, rounded, prominent with well-defined margins, almost twice as long as the inner metatarsal tubercle (OMTL/IMTL ratio 1.90).

Skin on dorsum smooth skin with few tiny tubercles at head base and on lateral sides of the dorsum (Fig. 7D). Dorsal surfaces of forelimbs smooth. Dorsal surfaces of hindlimbs with sparse tiny tubercles scattered on thighs and shanks (Fig. 16A). Upper eyelid smooth. Body flanks smooth, few tiny tubercles in tympanal region. Ventral surfaces of body and limbs completely smooth (Fig. 16B). Cloacal opening unmodified, directed posteriorly.

Coloration in life. Dorsal background coloration in life rusty-bronze with indistinct grayish-brown blotch corresponding to the “teddy-bear”-pattern in the middle of the dorsum (Fig. 7D). Dorsal “teddy-bear”-pattern is thus almost indistinct and has faint and irregular borders. Tiny rusty-red spots scattered across the dorsum and the dorsal surfaces of the hindlimbs (Fig. 7D). An indistinct rusty-brown interorbital band in the shape of an irregular blotch with indistinct borders runs across the head between the posterior parts of the upper eyelids. Light postocular stripe or other markings in tympanal area or around axilla absent. A dark blotch at the head base connects the interorbital bar with the dark marking in the middle of the dorsum. Dark markings on dorsum have no light edging. The lateral sides of dorsum slightly lighter, grayish-bronze. A pair of black spots edged with light-brown located above the cloacal opening.

Body and head flanks slightly lighter than the dorsum. Loreal area grayish-bronze lacking dark markings, the upper jaw bronze with indistinct off-white and grayish mottling below the eye, snout uniformly dark olive-brown. Light postocular stripe or dark markings in the tympanal region absent. On forelimbs, there are no conspicuous stripes or spots; hindlimbs with 1–3 weak and indistinct brownish crossbars. Transverse crossbars on fingers and toes absent.

Ventral surfaces lightly colored; belly and chest dull yellowish-white, with a few irregular grayish spots and mottling on throat and along the jaw margins. Rare gray spots and mottling on the ventral surfaces of the limbs. Ventral surfaces of forelimbs yellowish-gray, and the ventral surfaces of hindlimbs greenish-yellow. Ventral surfaces of hands with brown mottling (Fig. 16D), feet with brownish blotches running from the tibiotarsal articulation to the web (Fig. 16C). Iris light-bronze with indistinct brown reticulation; a short black stripe below the pupil not reaching the ventral edge of the iris (Fig. 7D). Pupil round, black, outlined with a thin bronze circle.

Coloration in preservative. After two years in preservative, the coloration pattern described above did not fade, and dark markings on dorsal surfaces of body and limbs became more prominent, especially the brown transverse crossbars on the hindlimbs (Fig. 16). The dorsal background color faded to brown. Traces of rusty-brown markings were observed as faded patterns; rusty-red spots on dorsum and dorsal surfaces of hindlimbs faded completely. The characteristic dark blotches above the cloacal opening remain unchanged. The bright-yellow coloration of the ventral surfaces faded completely; the ventral surface turned light-beige, but

the gray markings on the chin are still visible as a light-gray mottling.

Variation. The individuals in the type series are all very similar in appearance. Individual differences in size and body proportions are presented in Tables 4 and 5. In two females, the body length (SVL) ranges from 30.93 to 33.23 mm ($n = 2$); in two males, the SVL was much smaller, 22.05–22.18 mm ($n = 2$). There were no significant differences in the coloration of male paratypes and females, except that males had a darker throat coloration. The background coloration of the dorsum varied from rusty-bronze to yellowish-bronze. There is a certain variation in the degree of development of dark dorsal markings among the individuals; the male paratypes ZMMU A-8017 and ZMMU A-8018 had somewhat darker and more contrasting dorsal patterns. In females, the dorsal pattern is generally duller with faint borders.

Etymology. The species epithet “*peninsularis*” is a Latin adjective in nominative singular, meaning “peninsular”, and is given in reference to the distribution of the new species, which is presently only known from the southern part of the Thai-Malay Peninsula in Trang Province of Thailand and Terengganu State of Malaysia. Recommended common names: “Peninsular narrow-mouthed frog” (English); “Nhái bầu bán đảo Mã Lai” (Vietnamese); “Malayskiy uzkorot” (Малайский узкорот, Russian); “Eung mae nao pak sun” (อีงแมทนาวปากสุน, Thai); “Katak mulut sempit semenanjung” (Malay).

Distribution. Currently, *M. peninsularis* **sp. nov.** is known only from two localities in the Thai-Malay Peninsula (Fig. 1): Trang Province of Thailand and Terengganu State of northern Peninsular Malaysia. However, the actual extent of distribution of the new species remains unknown, and though it is unlikely that *M. peninsularis* **sp. nov.** is widely distributed, the discovery of additional populations of this species from southernmost Thailand and Peninsular Malaysia is anticipated.

Natural history notes. *Microhyla peninsularis* **sp. nov.** inhabits lowland dipterocarp forest habitats, where it was recorded at elevations of 80–200 m a.s.l. (Fig. 17). The lowland dipterocarp forest at the type locality (at Pa Lean District, Trang Province, Thailand) was dominated by trees of the families Dipterocarpaceae (*Anisoptera costata* Korth., *Hopea odorata* Roxb., *Dipterocarpus gracilis* Blume, and *Parashorea stellata* Kurz), Dilleniaceae (*Dillenia indica* L., *D. pentagyna* Roxb.), and Moraceae (*Artocarpus chama* Buch.). All type specimens were collected at night from 19:00 to 23:00 h after heavy rains and were mostly recorded while sitting in leaf litter or on rotten logs nearby sandy, slow-moving streams. The diet and predators of the new species are unknown. At the type locality, *M. peninsularis* **sp. nov.** was found in sympatry with *M. heymonsi*, *M. mantheyi* Das, Yaakob & Sukumaran, 2007, *Kaloula latidisca* Chan, Grismer & Brown, 2014, *Micryletta* cf. *lineata* (Taylor, 1962) (Microhylidae), *Humerana miopus* (Boulenger, 1918), *Sylvi-*



Figure 17. Natural habitat of *Microhyla peninsularis* sp. nov. at Pa Lean District, Trang Province, Thailand, the lowland dipterocarp forest at the type locality. Photograph by P. Pawangkhanant.

rana cf. *malayana* Sheridan & Stuart, 2018 (Ranidae), and *Polypedates discantus* Rujirawan, Stuart & Aowphol, 2013 (Rhacophoridae).

Tadpole. Larval morphology and biology of the new species are unknown.

Advertisement call. The male advertisement call of the new species represents a series of rasping sounds resembling the sound of a ratchet; it was not recorded, and the call parameters remain unknown.

Comparisons. We here compare *M. peninsularis* sp. nov. with the six other members of the *M. bermorei* species group (*M. bermorei* sensu stricto, *M. malcolmi*, *M. sundaica* sp. nov. (described above), *M. darevskii*, *M. picta*, and *M. pulchra*). The main diagnostic characters separating the new species from its congeners are summarized in Table 5.

Microhyla peninsularis sp. nov. is distinguished from *M. bermorei* sensu stricto by having: smaller body size in both sexes (SVL 22.1–22.2 mm in males, 30.9–33.2 mm in females vs. 33 mm in male, 36.3–38.1 mm in females); finger I length greater than half of finger II length ($F1 > \frac{1}{2}F2$ vs. $F1 < \frac{1}{2}F2$); body habitus stocky (vs. slender); dorsomedial grooves on toe disks present (vs. weak); dorsal color rusty-bronze (vs. olive-brown); dark markings on the dorsum and dorsal surfaces of the head indistinct with faint borders (vs. dorsal “teddy-bear”-pattern and interorbital bar dark, contrasting, with light edging); limbs

generally have no dark transverse crossbars, or have 1–3 weak crossbars on thighs and shanks (vs. up to 5–6 dark crossbars on thighs); iris coloration bright bronze with brown reticulum and short vertical stripe down from the pupil not reaching the ventral edge of the iris (vs. bronze with a black reticulation and a distinct black stripe below the pupil reaching the ventral edge of the iris).

Microhyla peninsularis sp. nov. is distinguished from *M. malcolmi* by having: smaller body size in both sexes (SVL 22.1–22.2 mm in males, 30.9–33.2 mm in females vs. 33.2–41.8 mm in males, 36.0–43.8 mm in females); finger I length greater than half of finger II length ($F1 > \frac{1}{2}F2$ vs. $F1 < \frac{1}{2}F2$); body habitus stocky (vs. slender); dorsomedial grooves on toe disks present (vs. absent); slightly less developed foot webbing (webbing formulae: $11-111-2111-11v2-1v$ vs. $11-1111-1111-11v1-1v$); dorsal color rusty-bronze (vs. gray-brown); dark markings on the dorsum and dorsal surfaces of the head indistinct with faint borders (vs. dorsal “teddy-bear”-pattern and interorbital bar dark, contrasting, with light edging); limbs generally have no dark transverse crossbars, or have 1–3 weak crossbars on thighs and shanks (vs. up to 3–4 dark crossbars on thighs); iris coloration bright bronze with brown reticulum and short vertical stripe down from the pupil not reaching the ventral edge of the iris (vs. bronze with black reticulation and a distinct black stripe below the pupil reaching the ventral edge of the iris).

Microhyla peninsularis sp. nov. is distinguished from *M. sundaica* sp. nov. (described above) by having: smaller body size in males (SVL 22.1–22.2 mm vs. 27.5–

27.9 mm); dorsal color rusty-bronze (vs. gray-bronze with grayish tint); dark markings on the dorsum and dorsal surfaces of the head indistinct with faint borders (vs. gray-brown dorsal “teddy-bear”-pattern distinct, edged with beige or white, anteriorly connecting with the dark interorbital bar); limbs generally have no dark transverse crossbars, or have 1–3 weak crossbars on thighs and shanks being more notable in preservation (vs. dorsal surfaces of forelimbs without prominent crossbars, hindlimbs with 2–3 dark-brown crossbars on thighs and shanks); iris coloration bright bronze with brown reticulum and short vertical stripe down from the pupil not reaching the ventral edge of the iris (vs. gray-bronze without reticulation or dark stripe below the pupil).

Microhyla peninsularis sp. nov. is further distinguished from *M. darevskii* by having: smaller body size in males (SVL 22.1–22.2 mm vs. 27.0–32.6 mm); by finger disks present (vs. absent); by slightly less developed foot webbing (webbing formulae: I1-I1I1-2III1-1IV2-1V vs. I1-I1I1-1III1-1IV1-1V); by dorsal color rusty-bronze (vs. brown); by having bright yellow coloration of belly with irregular grayish spots (vs. no yellow color on belly); iris coloration bright bronze with brown reticulum and short vertical stripe down from the pupil not reaching the ventral edge of the iris (vs. golden with a black reticulation and a distinct black stripe below the pupil reaching the ventral edge of the iris).

Microhyla peninsularis sp. nov. further differs from *M. picta* by having: smaller body size in males (SVL 22.1–22.2 mm vs. 25.2–30.1 mm); body habitus stocky with comparatively longer legs; tibiotarsal articulation of adpressed limb reaches well beyond snout (vs. stout with shorter legs; tibiotarsal articulation of the adpressed limb reaches the eye-snout level); finger I length greater than half of finger II length ($F1 > \frac{1}{2}F2$ vs. $F1 < \frac{1}{2}F2$); finger disks present (vs. absent); toe disks present and dorso-medial grooves on toes (vs. absent); tibiotarsal articulation reaching well beyond snout (vs. to the eye level); by greater development of foot webbing (webbing formulae: I1-I1I1-2III1-1IV2-1V vs. I2-2 $\frac{3}{4}$ I11 $\frac{3}{4}$ -2 $\frac{3}{4}$ III2 $\frac{3}{4}$ -3 $\frac{3}{4}$ IV4-2 $\frac{1}{2}$ V); dorsal coloration rusty-bronze (vs. sandy-brown); by having bright yellow coloration of belly with irregular grayish spots (vs. no yellow color on belly); limbs generally have no dark transverse crossbars, or have 1–3 weak crossbars on thighs and shanks being more notable in preservation (vs. brown transverse bars); iris coloration bright bronze with brown reticulum and with short vertical stripe down from the pupil (vs. golden with a black reticulation and with a distinct vertical dark stripe).

Microhyla peninsularis sp. nov. can be further differentiated from *M. pulchra* by having: skin on dorsum smooth with tiny scarce tubercles (vs. completely smooth); finger I length greater than half of finger II length ($F1 > \frac{1}{2}F2$ vs. $F1 < \frac{1}{2}F2$); finger disks present (vs. absent); toe disks and dorso-medial grooves on toe disks present (vs. absent); tibiotarsal articulation reaching well beyond snout (vs. to snout or just beyond); greater development of foot webbing (webbing formulae: I1-I1I1-2III1-1IV2-1V vs. I1 $\frac{1}{2}$ -2II1-3III2-3 $\frac{1}{4}$ IV3 $\frac{1}{2}$ -2V), numerous undulating bands and lines on dorsum absent (vs. present); belly

color yellowish with irregular grayish spots (vs. greenish-yellow lacking grayish spots); limbs generally have no dark transverse crossbars, or have 1–3 weak crossbars on thighs and shanks being more notable in preservation (vs. numerous brownish transverse crossbars); iris coloration bright bronze with brown reticulum and with short vertical stripe down from the pupil (vs. grayish with a black reticulation and with a distinct vertical dark stripe).

Discussion and Conclusions

Updated taxonomy of *Microhyla berdmorei* complex and unresolved issues

For many decades, the genus *Microhyla* has been one of the most taxonomically challenging groups of the Asian frog fauna. Due to the high degree of morphological similarity, small body size, and overlapping distributions of many *Microhyla* species, the taxonomy of this genus has always remained debatable (Poyarkov et al. 2014). Taxonomic issues involving wide-ranging species of *Microhyla* have been especially challenging. Though several such taxa were recently recognized as species complexes (e.g., Yuan et al. 2016; Garg et al. 2019; Nguyen et al. 2019; Poyarkov et al. 2019, 2020a, 2020b, 2020c; Gorin et al. 2020; Hoang et al. 2022), the inter- and intraspecific classification of others, including *M. berdmorei*, has remained controversial (Dubois 1987; Fei et al. 2009, 2010, 2012; Matsui et al. 2011; Garg et al. 2019; Gorin et al. 2020). In this study, we provide an integrative taxonomic analysis of the *M. berdmorei* species complex. Based on previously available and newly obtained molecular (mtDNA, nuDNA, and ddRAD-seq) and morphological data collected for a comprehensive sampling covering almost the entire range of the *M. berdmorei* complex, we were able to provide a significant revision of its taxonomy.

According to our results, *M. berdmorei* represents a complex that we herein delimited into four species that exhibit a substantial degree of genetic and morphological differentiation and can be readily diagnosed in the field and in collections. The two large-sized members of the *M. berdmorei* complex include *M. berdmorei* sensu stricto, which we restrict to Myanmar, Bangladesh, and Northeast India, and *M. malcolmi*, which we revalidate as with a species status for the populations of Indochina, including Vietnam, Laos, Cambodia, Thailand, extreme northern Peninsular Malaysia, and, presumably, the southernmost part of Yunnan Province of China. We provide further evidence regarding *Callula natatrix* as a subjective junior synonym of *M. berdmorei*, and regarding *M. fowleri* as a subjective junior synonym of *M. malcolmi*. We further assessed the status of Sundaland populations previously assigned to *M. berdmorei*. Our analyses revealed two lineages that belong to the *M. berdmorei* complex and feature comparatively smaller sized individuals, which we describe as two new species: *M. peninsularis* sp. nov. (for

the populations from the Thai-Malay Peninsula) and *M. sundaica* **sp. nov.** (for the populations from Peninsular Malaysia, Sumatra, and Borneo).

It is noteworthy that the four taxa of the *M. berdmorei* species complex exhibit relatively low values of genetic differentiation in the 16S rRNA mtDNA gene, a widely used marker for species delimitation in amphibians (Vieites et al. 2009). The mean genetic distance between the members of the *M. berdmorei* complex varied from 1.5% to 3.8% of substitutions in 16S rRNA sequences, which is generally lower than the recommended formal threshold of $p = 3.0\%$, traditionally considered an indication of species-level differentiation in amphibians (Vences et al. 2005a, 2005b). As we discussed above, however, there are many instances of valid species (as inferred from direct evidence for reproductive isolation) with 16S divergence that fall below this threshold (see e.g., Scherz et al. 2017; Dufresnes and Litvinchuk, 2022). Here, the evolutionary divergence of the candidate species lineage documented in the *M. berdmorei* species complex is robustly confirmed by the genome-wide nuclear differentiation and in respect to the body shape of individuals assigned to these lineages, as shown by the multivariate analysis of morphological characters (see Results). The case of the *M. berdmorei* complex thus adds to an increasing body of literature that suggest that the formal threshold of $p = 3.0\%$ in the 16S rRNA gene, as proposed by Vences et al. (2005a, 2005b) should not be regarded as a hard threshold for species delimitation. In fact, the values reported here generally exceed the minimal interspecific distances among other *Microhyla* species (Poyarkov et al. 2019, 2020b, 2020c; Gorin et al. 2020), as well as in some other microhylid frogs (e.g., Vassilieva et al. 2014).

Recently, a number of studies demonstrated that short fragments of the 16S rRNA gene were insufficient to retrieve correct tree topologies, for use in species delimitations in amphibians (Xia et al. 2012; Rockney et al. 2015; Chan et al. 2022). Although useful to detect potential candidate species, mtDNA divergence alone should not be regarded as sufficient evidence for species delimitation (Hillis 2019; Dufresnes and Jablonski 2022; Dufresnes et al. 2023; Vences et al. 2024; Wüster et al. 2024), since mtDNA fragments only represents a tiny portion of the molecular background of individuals, one that experience an independent demographic and evolutionary trajectory compared to the rest of the genome (Toews and Brelsford 2012; Bonnet et al. 2017). As we have implemented here, mitochondrial analyses should be ideally complemented by multilocus nuclear analyses, such as genome-reduction methods (e.g., ddRAD-seq, target-capture), whenever possible to elaborate more reliable species delimitation framework in anuran species complexes than currently permitted by traditional practices (Dufresnes et al. 2023; Vences et al. 2024).

The status of the type specimens of *M. berdmorei* remain confusing. Anderson (1871) and Sclater (1892) listed three specimens, ZSI 9718–9720, from “Arakan” (now in Rakhine State, Myanmar), as syntypes, although Blyth (1856) in the original description provided measurements for a single specimen. However, Theobald

(1873) commented that specimens from “Arakan” cannot represent the types of *M. berdmorei* since these were collected from “Schwe Gyen” (now Shwegyin Township, Bago Region, Myanmar), based on available records (see also Chanda et al. 2000; Dinesh et al. 2009). According to Garg et al. (2019), three poorly preserved specimens, ZSI 9718 (SVL 35.2 mm), ZSI 9719 (SVL 32.2 mm), and ZSI 9720 (SVL 33.3 mm), currently stored at ZSI (Kolkata, India), largely match the original description and other sampled populations of *M. berdmorei* from India. Therefore, pending formal specimen identification (e.g., using molecular tools or multivariate morphological analyses), the future designation of one of the three Indian specimens (ZSI 9718–9720) as a lectotype of *M. berdmorei*, should ensure the taxonomic stability of this species.

Many aspects of the *M. berdmorei* species complex taxonomy have yet to be clarified. Overall, the present paper recognizes the distribution of four species of the complex as parapatric; however, we cannot completely rule out cases of sympatric occurrence and/or hybrid zones between *M. malcolmi*, *M. peninsularis* **sp. nov.** and *M. sundaica* **sp. nov.**, particularly in the southernmost portion of Thailand and northern Peninsular Malaysia, where the minimum distance between the recorded localities of two species is approximately 25 km (in Trang Province, Thailand).

It should be noted that the bioacoustic variation among the *M. berdmorei* complex still remains to be investigated. Differences in advertisement call parameters are widely recognized as important signals of species-level divergence in Anura (e.g., Vieites et al. 2009), as successfully applied in *Microhyla* taxonomy (see Garg et al. 2019). However, the only published work describing the call parameters for the *M. berdmorei* complex members remains the study by Heyer (1971), in which he provided a brief description of the advertisement call of *M. malcolmi* from Thailand (mentioned as *M. berdmorei* in his work; see review by Poyarkov et al. 2019). Herein we presented a preliminary analysis of male advertisement call variation among three out of four species of the *M. berdmorei* complex; bioacoustic data for *M. peninsularis* **sp. nov.** is still lacking. Our analysis revealed stable differences in call peak frequencies of the *M. berdmorei* complex members, which only slightly overlapped: *M. malcolmi* had the lowest Fpeak values (1631 ± 93 Hz; range 1507–1809 Hz), *M. berdmorei* was estimated to have a higher Fpeak (1892 ± 82 Hz; range 1781–1969 Hz), while *M. sundaica* **sp. nov.** had the highest Fpeak values (2029 ± 106 Hz; range 1898–2203 Hz). Perhaps the more significant bioacoustic difference among the three species is the shape of relative amplitude profiles of the individual calls, which was almost symmetrical in *M. berdmorei* (maximum amplitude reaches peak in the middle of the call), in contrast to *M. malcolmi* (maximum amplitude reaches peak in the beginning of the call, then gradually decreases) and *M. sundaica* **sp. nov.** (call contains two syllables: the introductory note with lower relative amplitude and frequency, and the main call with relative amplitude and frequency increasing towards the call’s end). However, due to the limited number of recordings available for

analysis and their relatively poor quality, we should approach our data cautiously. Further comprehensive bio-acoustic research is necessary to estimate the variation of advertisement call parameters among the *M. berdmorei* complex members.

Biogeography of *Microhyla berdmorei* complex members

The timeframe of diversification in the *M. berdmorei* complex largely corroborate previously obtained divergence time estimates by Gorin et al. (2020), although the 95% Highest Posterior Density Intervals (HPD) reported in our paper are notably wider than in Gorin et al. (2020), likely due to a more imbalanced taxon sampling across the whole genus. Nevertheless, our estimations of median node heights still provide important ground for comparative analysis of cladogenetic events in *Microhyla*. Specifically, we showed that the *M. berdmorei* species complex evolved independently from other *Microhyla* clades since the early Miocene (ca. 19.7 mya), and diversified during the late Miocene (ca. 7.5 mya), with the divergence between the two pairs of sister species (*M. berdmorei* – *M. malcolmi* vs. *M. peninsularis* **sp. nov.** – *M. sundaica* **sp. nov.**) dated around 5.2–5.7 mya. Gorin et al. (2020) examined the historical biogeography of *Microhyla* and suggested that the common ancestor of the *M. berdmorei* complex likely originated in the Thai-Malay Peninsula or western Indochina. Indeed, the Thai-Malay Peninsula hosts the highest diversity of *M. berdmorei* complex members (three out of four species), which corroborates the assumption by Gorin et al. (2020).

The distribution of the four *M. berdmorei* complex members is geographically circumscribed, with two large-bodied species (*M. berdmorei* sensu stricto, *M. malcolmi*) being restricted to the mainland of Southeast Asia, while two small-bodied species (*M. peninsularis* **sp. nov.**, *M. sundaica* **sp. nov.**) occurring in the Sundaic Region. *Microhyla berdmorei* sensu stricto is widely distributed in the Indo-Burma Region, and according to our data, it is reliably recorded in India, Bangladesh, and Myanmar. Our mtDNA analysis revealed two subclades within *M. berdmorei* sensu stricto, one of which is restricted to the western slopes and foothills of the Arakan Mountains in Myanmar and the adjacent hilly areas of Bangladesh and Northeast India (subclade B1, see Fig. 1). The second subclade of *M. berdmorei* sensu stricto occurs in the Irrawaddy (or Ayeyarwady) River Valley and southern Myanmar lowlands (subclade B1, see Fig. 2); the two subclades are likely separated by the Arakan Mountain Range. Due to insufficient sampling of *M. berdmorei* sensu stricto from the Myanmar portion of Tenasserim (Tanintharyi Region), the actual extent of its distribution eastwards remains unknown. It is highly likely that the ranges of *M. berdmorei* sensu stricto and *M. malcolmi* are separated by the valley of the Salween (or Thanlwin) River. Since the Salween River is one of the largest rivers in Southeast Asia, it may act as a physical barrier or a biogeographic filter (McKenna 1973; Das 1996). The

key role of the Salween River as a line of biogeographic turnover was recently demonstrated in a number of other organisms, such as herbaceous perennial plants (Li et al. 2011), *Draco* flying lizards (Klabacka et al. 2020), and pitviper snakes (Idiattullina et al. 2024).

Microhyla malcolmi is widely distributed across Indochina and even penetrates southwards of the Isthmus of Kra, as this species reaches extreme southern Thailand (Yala and Narathiwat provinces) and the northernmost state of Malaysia (Perlis State). Both mtDNA and ddRAD-seq revealed phylogeographic structure within *M. malcolmi*, with the populations from the Thai-Malay Peninsula south of the Isthmus of Kra forming a clade sister to all remaining populations from the mainland Indochina (subclade A3, see Figs 1–3). This further underlines the importance of the Isthmus of Kra as a biogeographic barrier for Indochinese herpetofauna (Poyarkov et al. 2021, 2023). On the mainland of Indochina, *M. malcolmi* includes two moderately supported subclades, one of which is restricted to the southern Indochinese lowlands: southern Vietnam and East Thailand (subclade A2, see Fig. 1). The second subclade is widely distributed in the hills of northern and central Indochina, including central Vietnam, Laos, and northern Thailand (subclade A1, see Fig. 1). Furthermore, we also noticed that the distribution of *M. malcolmi* in northern Vietnam is likely limited from the north by the Red River Valley (Fig. 1), which is a famous biogeographic barrier (e.g., Yuan et al. 2016; Poyarkov et al. 2021, 2023). The two subclades of *M. malcolmi* A1 and A2 are recorded in the near sympatric conditions in eastern Thailand (Khao Yai NP, Nakhon Ratchasima Province, locality 23 in Fig. 1) and in the Central Highlands of Vietnam (Kon Chu Rang NR, Gia Lai Province, localities 12–13 in Fig. 1). The low values of nodal support of subclades A1 and A2, as well as for the corresponding branches in the ddRAD-seq phylogenomic analysis (Fig. 3) suggest shallow population structure that shall be clarified by population genetic analyses to elucidate the phylogeography of *M. malcolmi* in Indochina.

Both *M. peninsularis* **sp. nov.** and *M. sundaica* **sp. nov.** occur in the Sundaic Region, southwards of the Isthmus of Kra and the Ta-Pi - Khlong Marul Fault Line (see Poyarkov et al. 2018b, 2021, 2023). *Microhyla peninsularis* **sp. nov.** is currently known only from two localities – one in Trang Province of southern Thailand and one from Terengganu State of Malaysia (see below). Despite their geographic proximity, these populations are separated by a substantial 16S divergence (subclades D1 and D2; $p = 1.2\%$, range 1.21%–1.22%). Despite our intensive survey efforts in southern Thailand, we failed to discover additional populations of *M. peninsularis* **sp. nov.** According to our data, *M. sundaica* **sp. nov.** includes three mitochondrial subclades: subclade C1 occurs in Peninsular Malaysia south of the Kangar-Pattani Line (Poyarkov et al. 2021, 2023); subclade C2 is restricted to Sumatra; and subclade C3 is found on Borneo (see Fig. 2B). We could not examine specimens from Sumatra and Borneo and were not able to examine the degree of morphological differentiation of *M. sundaica* **sp. nov.** populations.

Given the substantial degree of 16S differentiation ($p = 0.8\%–2.1\%$) and geographic separation of these lineages, they may warrant taxonomic recognition, perhaps at the subspecies rank in the future. The last words on the diversity of the diversity of the *M. berdmorei* complex in Sundaland are thus left to be written.

Several existing reports on the distribution of the *M. berdmorei* species complex members remain highly controversial. We review some of these cases below. Lalrem-sanga et al. (2007) reported *M. butleri* (body size range: SVL 20–25 mm in males, 21–26 mm in females; see Nguyen et al. 2019; Poyarkov et al. 2014, 2020b, 2020c) from Mizoram State, India, without providing any information on vouchers or the sex of collected specimens, but noting a much larger body size of SVL 31–34 mm. Therefore, the taxonomic status of this record was subsequently questioned by Garg et al. (2019). One of the authors of the present manuscript (HTL) confirms that this record was based on a misidentification of *M. berdmorei* sensu stricto.

Teynié et al. (2010: fig. 3A) reported “*M. berdmorei*” from Lake Maninjau, Sumatera Barat Province, Indonesia, based on two specimens (both of unknown sex): MNHN 2003.3374 (SVL 15.0 mm) and MNHN 2003.3375 (SVL 14.9 mm). However, based on color pattern and size, the reported specimens most likely belong to the *M. palmipes* group, with the following key diagnostic characters: small-sized frogs (male SVL 16.0 mm) with lateral nostril orientation; weak disks on digits lacking terminal grooves; moderately developed webbing on toes; and inner and outer metatarsal tubercles small (Bain and Nguyen 2004; Poyarkov et al. 2014). This group presently includes a single species, *M. palmipes* Boulenger, 1897, from Java, Sumatra, and adjacent offshore islands in Indonesia. Therefore, a re-examination of the taxonomic status of these two specimens (MNHN 2003.3374–75) is required to clarify the status of this record.

Matsui et al. (2011) assigned the population from Besut District, Trengganu State, Malaysia (KUHE 52373) to “*M. berdmorei*”, as well as the populations from Gombak, Selangor State, Malaysia (KUHE 52034), Bengkulu Province, Sumatra, Indonesia (MZB 16413), and Paramasan, Kalimantan Province, Indonesia (MZB 15270). This taxonomy was subsequently followed by Garg et al. (2019), Li et al. (2019), Gorin et al. (2020), and Kundu et al. (2021). Based on the molecular analysis in our study (Figure S1), we propose that the specimen KUHE 52373 should be re-identified as *M. peninsularis* sp. nov. In contrast, three specimens (KUHE 52034, MZB 16413, and MZB 15270) should be re-identified as *M. sundaica* sp. nov. A re-examination of the morphology of these specimens is also required to confirm their taxonomic status.

Conservation issues

Currently, *M. berdmorei* sensu lato is listed as Least Concern (LC) due to its wide distribution, high tolerance to habitat modification, and presumed large population

(IUCN 2022). As all members of the *M. berdmorei* species complex, including the two new species, *M. peninsularis* sp. nov. and *M. sundaica* sp. nov., are typical inhabitants of lowly and hilly tropical and subtropical forests, they may all suffer from the progressing deforestation affecting Asian forests. However, given the presumably large area of occurrence, we propose to list the following three species: *M. berdmorei* sensu stricto, *M. malcolmi* and *M. sundaica* sp. nov., as Least Concern (LC) species based on the IUCN Red List criteria (IUCN 2019). *Microhyla peninsularis* sp. nov. is currently known only from two localities in Thailand and Malaysia. Given the scarcity of available natural history information on this species, we propose to list *M. peninsularis* sp. nov. as Data Deficient (DD) species based on the IUCN Red List criteria (IUCN 2019). Further work is required to clarify the population status and the extent of distribution of *M. peninsularis* sp. nov.

With this contribution, the alpha-taxonomy of the *M. berdmorei* species complex is significantly revised. Importantly, the molecular evidence combined traditional DNA barcoding analyses to identify and map candidate taxa, with high-throughput sequencing to confirm the nuclear differentiation of this taxa, an integrative approach now seen as high standard in taxonomy (Miralles et al. 2024; Vences et al. 2024). However, a major gap in our current knowledge is the distributional boundaries of each species, and their degree of genetic isolation in the face of potential hybridization at secondary contact, as well as the evolutionary and taxonomic significance of their intraspecific diversity. Future research should further focus on determining the distribution, elevation range, population trends, natural history, and conservation status of the members of the *M. berdmorei* species complex, particularly the two new species described herein.

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Supplementary Material 1

Tables S1–S7

Authors: Trofimets AV, Dufresnes C, Pawangkhanant P, Bragin AM, Gorin VA, Hasan M, Lalremsanga HT, Muin MA, Le DX, Nguyen TV, Suwannapoom C, Poyarkov NA (2024)

Data type: .pdf

Explanation notes: **Table S1.** Sequences and voucher specimens of the *Microhyla berdmorei* complex and outgroup taxa used in this study. Locality number corresponds to those shown on the map in Figure 1. An asterisk (*) indicates the specimens included in the ddRAD-seq analysis. — **Table S2.** Morphometric characters recorded from each specimen of *M. berdmorei* sensu stricto and *M. malcolmi* examined. (Continues on the next page). — **Table S3.** Primers used in this study. “F,” “L”—forward primer, “R,” “H”—reverse primer. — **Table S4.** Characteristics of analyzed single-marker DNA sequences and the proposed optimal evolutionary models for gene and codon partitions as estimated in PartitionFinder v1.0.1. Total length (in bp), number of conservative (Cons.), variable (Var.) and parsimony informative (Pars.-Inf.) sites, estimated Transition/ Transversion bias (R), and nucleotide frequencies (in %) are given (data presented only for the ingroup). The optimal partitioning scheme and model fit was estimated as suggested by the Akaike information criterion (AIC). — **Table S5.** Outgroup taxa used for divergence time estimation in *Microhyla berdmorei* complex. — **Table S6.** Calibration points for divergence time estimation. Node – tree node used for calibration, for node names see Figure S3; divergence time given in millions years (Ma). — **Table S7.** Summary of PC scores and statistics for the Principal Components Analysis (PCA) consisting of members of the *Microhyla berdmorei* species complex. Abbreviations are listed in the materials and methods.

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Link: <https://doi.org/10.3897/vz.74.e127937.suppl1>

Supplementary Material 2

Figures S1, S2

Authors: Trofimets AV, Dufresnes C, Pawangkhanant P, Bragin AM, Gorin VA, Hasan M, Lalremsanga HT, Muin MA, Le DX, Nguyen TV, Suwannapoom C, Poyarkov NA (2024)

Data type: .zip

Explanation notes: **Figure S1.** Phylogenetic relationships of the *Microhyla berdmorei* species group. B: ML-inference tree of *Microhyla* derived from the analysis of 3119 bp of concatenated alignment including 12S rRNA, tRNA^{Val}, 16S rRNA, and COI mtDNA gene fragments. For voucher specimen information and GenBank accession numbers see Table S1. Numbers at tree nodes correspond to ML UFBS/BIPP support values, respectively. The color of the mitochondrial lineages in the tree corresponds to the color used in Figures 1–5. — **Figure S2.** Time tree of the *Microhyla berdmorei* complex. BEAST chronogram on the base of 3588 bp-long mtDNA + nuDNA dataset (12S rRNA, tRNA^{Val}, 16S rRNA, and COI mtDNA genes + BDNF gene). Values at tree nodes correspond to median divergence age estimates; blue bars at tree nodes correspond to 95% HPD of divergence age estimates.

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