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Phylogeographic pattern and taxonomic revision of the *Kaloula baleata* species complex (Amphibia, Anura, Microhylidae) with description of two new species from Indochina

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Abstract

Despite increased attention by molecular taxonomists, the herpetofauna of Southeast Asia still hides many undescribed species among far-ranging taxa. In this study, we re-examine the mitochondrial diversity of painted frogs of the microhylid genus *Kaloula*, based on ~2,455 bp of published and new 12S and 16S rRNA sequences, and describe two new species from the tropical forests of southern Vietnam and central Laos based on integrative evidence. These species, which belong to the *K. baleata* complex, feature species-level mitochondrial divergence (> 4.4% at 16S rRNA) and are both morphologically well-differentiated from each other and from the recently described *K. indochinensis*, to which they were previously confounded. Comparative examinations also indicate distinct male advertisement calls and unique coloration features. Based on genetic barcoding, we preliminarily revise the species distribution ranges in the *K. baleata* complex, which support a general pattern of biogeographic partitioning that has been widely retrieved among the Indochinese amphibians studied so far. Molecular diversity within *K. baleata* further suggests genetic structure across Sundaland, namely three shallow mitochondrial haplogroups worthy of fine-scale phylogeographic and taxonomic investigations. Furthermore, our study highlights the propensity of amphibian species "hidden in plain sight," even among recently studied taxa, thus calling for caution when specifying type specimens—the type series of *K. indochinensis*, described in 2013, includes specimens of the one of the new species. Our study emphasizes the continued need for thorough herpetological surveys even in supposedly well-known parts of Indochina and sets the ground for future research in *Kaloula* painted frogs, notably to test evolutionary and taxonomic hypotheses with genomic loci.

Key Words

16S rRNA, bioacoustics, DNA barcoding, Laos, morphology, Southeast Asia, systematics, taxonomy, Vietnam

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PENSOFT.

Introduction

Many widely distributed amphibian genera in Asia have undergone a considerable increase in their numbers of recognized species since the turn of the 21st century. For example, among microhylids of the genus *Microhyla* Tschudi, 1838, the number of recognized species jumped from 22 to 51 within two decades (Poyarkov et al. 2020a; Zhang et al. 2022; Trofimets et al. 2024). The number of species within the genus *Micryletta* Dubois, 1987, rose from three in the 20th century to 13 species nowadays (Suwannapoom et al. 2020; Poyarkov et al. 2021a; Sankar et al. 2022). The genus *Kalophrynus* Tschudi, 1838, included from 13 to currently 27 recognized species (Fukuyama et al. 2021). Two new microhylid genera were discovered in Southeast Asia in the past several years, namely, *Siamophryne* Suwannapoom, Sumontha, Tunprasert, Ruangsuwan, Pawangkhanant, Korost & Poyarkov, 2018 (one single known species) and *Vietnamophryne* Poyarkov, Suwannapoom, Pawangkhanant, Aksornneam, Duong, Korost & Che, 2018 (six species described so far; see Suwannapoom et al. 2018; Poyarkov et al. 2018a, 2021b; Gorin et al. 2021; Frost 2024).

Quite a few genera of Asian microhylids, however, have so far evaded the focus of taxonomic studies, and their species numbers thus remained relatively stable. One notable example is the genus *Kaloula* Gray, 1831, also known as Asian painted frogs (Frost 2024). *Kaloula* is a widely distributed genus of microhylids, with 18 species recognized up to date. Painted frogs inhabit East Asia, from Korea and northeastern China to Southeast Asia, including Indochina to the Sunda Islands and the Philippines to the south, and Bangladesh and northeastern India to the west (Othman et al. 2022; Frost 2024). The genus *Kaloula* is characterized by the following morphological attributes: pupil round; tongue oval, entire, and free behind; two transverse ridges across the palate in front of the pharynx; a strong bony ridge behind each choanae; the first finger shorter than the second and the outer toe shorter than the third; medium body size (SVL 35–60 mm); smooth or slightly rough dorsum with irregular dark markings; tips of the fingers dilated into disks and truncated; fingers free of the web; nearly full webbing on toes in males and reduced webbing in females (e.g., Gray 1831; Sengupta et al. 2009; Gorin et al. 2021). Recent contributions to the diversity of this genus include the review by Blackburn et al. (2013), which focused on *Kaloula* species inhabiting Southeast Asian islands, mainly the Philippine Archipelago. In this study, the authors conducted phylogenetic analysis on 140 *Kaloula* individuals from all over Southeast Asia and indicated the presence of at least six undescribed lineages of putative species status. Following the study of Blackburn et al. (2013), two new species of the *K. baleata* complex were described from Indochina, namely *K. indochinensis* Chan, Blackburn, Murphy, Stuart, Emmett, Ho & Brown, 2013 (Chan et al. 2013), and from Peninsular Malaysia, namely *K. latidisca* Chan, Grismer & Brown, 2014 (Chan et al. 2014). In both cases, authors provided only limited morphological data to substantiate species divergence, did not provide any bioacoustic data, and based their phylogenetic estimations entirely on the previously published mtDNA data of Blackburn et al. (2013).

In parallel, a new species, *K. nonggangensis* Mo, Zhang, Zhou, Chen, Tang, Meng & Chen, 2013, was described from the Guangxi Province of China (Mo et al. 2013) on the basis of morphological and genetic data. More recently, the subspecies *K. baleata ghoshi* Cherchi, 1954, endemic to the Andaman Islands, was elevated to full species status based on morphological differentiation, accompanied by new data on natural history, bioacoustics, and distribution (Chandramouli and Prasad 2018). Lastly, the phylogeography of the genus *Kaloula* in East Asia was re-summarized by Ohtman et al. (2022), based mostly on previously published data, and without emphasizing undescribed diversity.

In this work, we present an updated mitochondrial DNA (hereafter mtDNA)-based genealogy for the genus *Kaloula*, combining sequences available in GenBank with new sequences obtained from an extensive sampling in Indochina, as well as integrative taxonomic revisions in the *K. baleata* species complex, specifically for two populations from central Laos and southern Vietnam previously assigned to *K. indochinensis* (Chan et al. 2013). These populations are deeply divergent in the mitochondrial phylogeny and feature morphological and bioacoustic differentiation from related taxa, hence substantiating their description as new species.

Materials and methods

Sample collection

Fieldwork in Vietnam was conducted by NAP, AMB, and VAG in 2009–2023; fieldwork in Laos was conducted by NLO and KDM in 2009. We obtained geographic coordinates and elevation data using a Garmin GPSMAP 60CSx (USA) and recorded them in the WGS84 datum. The specimens collected were initially fixed in 4% formalin for 24 h and later transferred to 75% ethanol for storage; muscle or liver tissues were taken prior to the fixation in formalin and preserved in 95% ethanol for genetic analysis. Specimens were subsequently deposited in the herpetological collections of the Zoological Museum of Lomonosov Moscow State University (ZMMU, Moscow, Russia) and of the Zoological Institute, Russian Academy of Sciences (ZISP, St. Petersburg, Russia).

Laboratory methods

For the molecular phylogenetic analyses, total genomic DNA was isolated using the standard phenol-chloroform-proteinase K extraction procedures with consequent isopropanol precipitation for a final concentration of about 1 mg/ml (protocols followed the works of Hillis et

al. 1996; Sambrook and Russell 2001). We visualized the isolated total genomic DNA using agarose electrophoresis in the presence of ethidium bromide. We measured the concentration of total DNA in 1 µL using NanoDrop 2000 (Thermo Scientific) and consequently adjusted it to ca. 100 ng DNA/µL.

We amplified mtDNA fragments covering the 16S rRNA gene and the adjacent tRNA genes to obtain a 1,003 bp-long continuous fragment. The 16S rRNA gene is widely used for biodiversity surveys in amphibians (Vences et al. 2005; Vieites et al. 2009) and has been analyzed in the most recent phylogenetic studies on Microhylinae (Matsui et al. 2011; Garg et al. 2019; Gorin et al. 2020, 2021). We performed DNA amplification in 20 µL reactions using ca. 50 ng genomic DNA, 10 nmol of each primer, 15 nmol of each dNTP, 50 nmol additional $MgCl_2$, Taq PCR buffer (10 mM Tris-HCl, pH 8.3, 50 mM KCl, 1.1 mM $MgCl_2$, and 0.01% gelatine), and 1 unit of Taq DNA polymerase. Primers used in PCR and sequencing include 16sL-2188 (CTGACCGTGCAAAGGTAGCGTAATCACT) and 16H-1 (CTCCGGTCTGAACTCAGATCACGTAGG) (Hedges et al. 1994; Matsui et al. 2005). The PCR conditions involved an initial denaturation step of 5 min at 94 °C, followed by 43 cycles of denaturation for 1 min at 94 °C, primer annealing for 1 min using the TouchDown program, reducing 1 °C every cycle, extension for 1 min at 72 °C, and a final extension step for 5 min at 72 °C (Gorin et al. 2020, 2021).

PCR products were loaded onto 1.0% agarose gels in the presence of ethidium bromide and visualized in agarose electrophoresis. When distinct bands were obtained, we purified PCR products using 2 µL of a 1:4 dilution of ExoSapIt (Amersham) per 5 µL of PCR product prior to cycle sequencing. A 10 µL sequencing reaction included 2 µL of template, 2.5 µL of sequencing buffer, 0.8 µL of 10 pmol primer, 0.4 µL of BigDye Terminator version 3.1 Sequencing Standard (Applied Biosystems), and 4.2 µL of water. The cycle sequencing used 35 cycles of 10 sec at 96 °C, 10 s at 50 °C, and 4 min at 60 °C. We purified the cycle sequencing products by ethanol precipitation. We carried out sequence data collection and visualization on an ABI 3730xl Automated Sequencer (Applied Biosystems). We deposited the obtained sequences in GenBank under the accession numbers PQ268497–PQ268520.

Phylogenetic analyses

To reconstruct the matrilineal genealogy, we used newly obtained 16S rRNA sequences of *Kaloula* spp. from Laos and Vietnam and the sequences of 12S rRNA and 16S rRNA mtDNA fragments of the *K. baleata* species complex members from Thailand, Malaysia, and Indonesia, as well as other *Kaloula* species obtained from GenBank. Table 1 summarizes the information on GenBank Accession Numbers, museum vouchers, and the locality of origin for the sequences used in this study. We also added sequences of *Uperodon taprobanicus* (Parker, 1934) as a sister group; a sequence of *Kalophrynus interlineatus* (Blyth, 1855) was used to root the tree; the final alignment included 2,455 bp. In total, we obtained data for 16S rRNA for 233 specimens, which included 15 out of 18 currently recognized *Kaloula* species, including the topotype specimens of *K. baleata* (Müller, 1836) (type locality: Java, Indonesia) (see Table 1); geographic distribution of the sampled populations of the *K. baleata* species complex is shown in Fig. 1.

We initially aligned nucleotide sequences using ClustalX 1.81 (Thompson et al. 1994) with default parameters and then optimized them manually in BioEdit 7.0.5.2 (Hall 1999) and MEGA 11.0 (Tamura et al. 2013). We utilized ModelFinder (Kalyaanamoorthy et al. 2017) to determine the most suitable evolutionary models for our data set analysis. According to the Akaike Information Criterion (AIC), the best-fitting models of DNA evolution for 12S rRNA, tRNA-Val, and 16S rRNA genes of mtDNA are GTR+I+G, K2P+G, and GTR+I+G, respectively. We determined mean uncorrected genetic distances (p-distances) between sequences with MEGA 11.0.

We inferred the matrilineal genealogy using Bayesian Inference (BI) and Maximum Likelihood (ML) approaches. We conducted BI using MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003). Metropolis-coupled Markov chain Monte Carlo (MCMCMC) analyses were run with one cold chain and three heated chains for one million generations and sampled every 1,000 generations. We performed two independent MCMCMC runs, and the initial 100 trees were discarded as burn-in. We assessed confidence in tree topology based on the frequency of nodal resolution (posterior probability; BI PP) (Huelsenbeck and Ronquist 2001). We used IQ-TREE (Nguyen et al. 2015) to reconstruct ML-trees. A total of 10,000 ultrafast bootstrap replications for ML analysis (UFB) (Minh et al. 2013) assessed the confidence in tree topology for ML analysis. In both datasets, we regarded tree nodes with BI PP and UFB values over 0.95 to be sufficiently resolved a priori. We considered BI PP and UFB values between 0.95 and 0.90 as tendencies. Lower values were considered to indicate unresolved nodes (Huelsenbeck and Hillis 1993; Minh et al. 2013).

Morphological analysis

Measurements were taken using a digital caliper under a light dissecting microscope to the nearest 0.01 mm, subsequently rounded to 0.1 mm. The adult morphometrics and character terminology follow Poyarkov et al. (2018b): (1) snout-vent length (SVL; measured from the tip of the snout to cloaca); (2) head length (HL; measured from the tip of snout to hind border of jaw angle); (3) snout length (SL; measured from the anterior corner of eye to the tip of snout); (4) eye length (EL; measured as the distance between anterior and posterior corners of the eye); (5) nostril-eye length (N-EL; measured as the distance between the anterior corner of the eye and the nostril center); (6) head width (HW; measured as the maximum width of head on the level of mouth angles in ventral view); (7) internarial

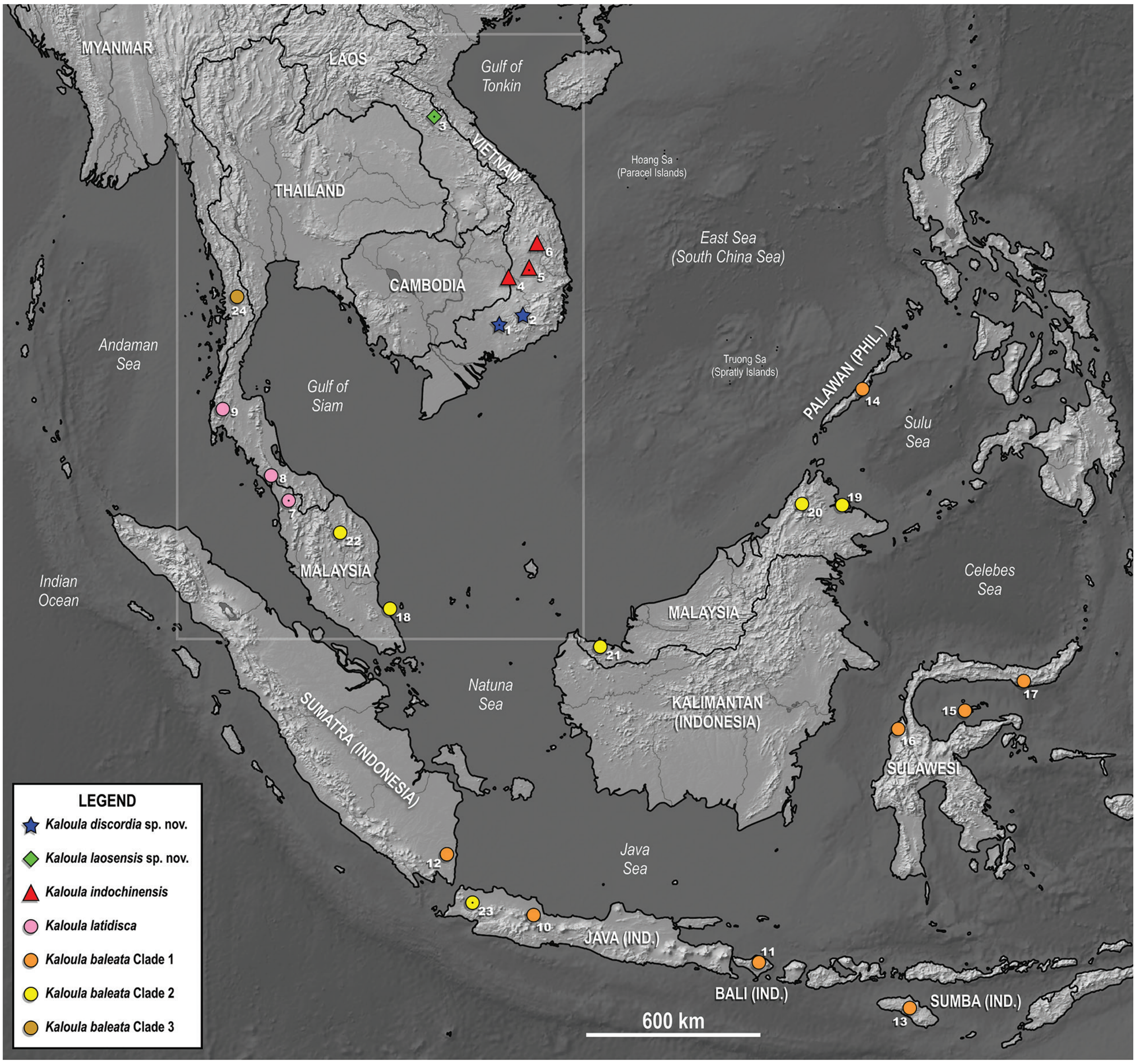

Figure 1. Geographic origins of the specimens of the *Kaloula baleata* species complex included in phylogenetic analyses. Dots in the symbols denote type localities. Symbol colors correspond to those used in Fig. 2. Numbers near symbols correspond to the locality numbers given in Table 1. The white rectangle represents the area of inset map detailing the distribution of the *K. baleata* species complex in Indochina in Fig. 5.

distance (IND; measured as the distance between the central points of nostrils); (8) interorbital distance (IOD; measured as the shortest distance between the medial edges of eyeballs in dorsal view); (9) upper eyelid width (UEW; measured as the maximum distance between the medial edge of eyeball and the lateral edge of upper eyelid); (10) tympanum length, measured as the horizontal tympanum diameter (TMP); (11) forelimb length (FLL; measured as the length of straightened forelimb to the tip of third finger); (12) lower arm and hand length (LAL; measured as the distance between elbow and the tip of third finger); (13) hand length (HAL; measured as the distance between the proximal end of outer palmar (metacarpal) tubercle and the tip of third finger); (14) first finger length (1FL, measured as the distance between the tip and the distal end of inner palmar tubercle); (15) inner palmar tubercle length (IPTL; measured as the maximum distance between proximal and distal ends of inner palmar tubercle); (16) outer palmar tubercle length (OPTL; measured as the maximum diameter of outer palmar tubercle); (17) third finger disk diameter (3FDD); (18) hindlimb length (HLL; measured as the length of straightened hindlimb from groin to the tip of fourth toe); (19) tibia length (TL; measured as the distance between the knee and tibiotarsal articulation); (20) foot length (FL; measured as the distance between the distal end of tibia and the tip of fourth toe); (21) first toe length (1TOEL), measured as the distance between the distal end of inner metatarsal tubercle and the tip of first toe; (22) fourth toe disk diameter (4TDD); (23) outer metatarsal tubercle length (OMTL). Webbing and subarticular tubercle formulas follow those of Savage (1975). We took all measurements on the right side of the examined specimen. We determined the sex of specimens by examining the presence of eggs in the abdomen of a dissected specimen.

Table 1. Museum voucher information, geographic localities, and GenBank accession numbers of specimens and sequences used in this study. Exact locality information is unknown for specimens obtained via the pet trade or those published in some earlier works. Locality numbers given in brackets in bold after the locality name correspond to the numbers shown in Fig. 1.

No.	Species	Locality	Museum / Sample ID	Accession numbers		Reference
	Ingroup			12S rRNA	16S rRNA	
***Kaloula baleata* species complex**						
1	*Kaloula discordia* sp. nov.	Vietnam, Dong Nai Prov., Cat Tien NP (**1**)	ZMMU-A-4642		PQ268510	this work
2	*Kaloula discordia* sp. nov.	Vietnam, Dong Nai Prov., Cat Tien NP (**1**)	ZMMU-A-4739		PQ268511	this work
3	*Kaloula discordia* sp. nov.	Vietnam, Dong Nai Prov., Cat Tien NP (**1**)	ZISP 15285		PQ268512	this work
4	*Kaloula discordia* sp. nov.	Vietnam, Dong Nai Prov., Cat Tien NP (**1**)	ZMMU-A-8134		PQ268513	this work
5	*Kaloula discordia* sp. nov.	Vietnam, Dong Nai Prov., Cat Tien NP (**1**)	ZMMU-A-8135		PQ268514	this work
6	*Kaloula discordia* sp. nov.	Vietnam, Lam Dong Prov., Loc Bac (**2**)	ZMMU NAP-02826		PQ268515	this work
7	*Kaloula discordia* sp. nov.	Vietnam, Lam Dong Prov., Loc Bac (**2**)	ZMMU NAP-03384		PQ268516	this work
8	*Kaloula laosensis* sp. nov.	Laos, Khammouane Prov., Nakai-Nam Theun NP (**3**)	ZISP 15284		PQ268517	this work
9	*Kaloula laosensis* sp. nov.	Laos, Khammouane Prov., Nakai-Nam Theun NP (**3**)	ZMMU-A-8144		PQ268518	this work
10	*Kaloula indochinensis*	Vietnam, Dak Lak Prov., Yok Don NP (**4**)	ZMMU-A-8147		PQ268497	this work
11	*Kaloula indochinensis*	Vietnam, Dak Lak Prov., Yok Don NP (**4**)	ZMMU-A-8148		PQ268498	this work
12	*Kaloula indochinensis*	Vietnam, Gia Lai Prov., Krong Pa (**5**)	ROM32925		KC180032	de Sa et al. 2012
13	*Kaloula indochinensis*	Vietnam, Gia Lai Prov., Krong Pa (**5**)	ZISP-Gia Lai 1		PQ268499	this work
14	*Kaloula indochinensis*	Vietnam, Gia Lai Prov., Krong Pa (**5**)	ZISP-Gia Lai 2		PQ268500	this work
15	*Kaloula indochinensis*	Vietnam, Gia Lai Prov., Krong Pa (**5**)	ROM32925	KC822572		Blackburn et al. 2013
16	*Kaloula indochinensis*	Vietnam, Gia Lai Prov., Krong Pa (**5**)	ROM32932	KC822573		Blackburn et al. 2013
17	*Kaloula indochinensis*	Vietnam, Gia Lai Prov., Krong Pa (**5**)	ROM32943	KC822574		Blackburn et al. 2013
18	*Kaloula indochinensis*	Vietnam, Gia Lai Prov., Kon Ka Kinh NP (**6**)	ZMMU-A-6315		PQ268501	this work
19	*Kaloula indochinensis*	Vietnam, Gia Lai Prov., Kon Ka Kinh NP (**6**)	ZMMU-A-6316		PQ268502	this work
55	*Kaloula latidisca*	Malaysia, Kedah, Gubir (**7**)	LSUHC5074	KC822576		Blackburn et al. 2013
56	*Kaloula latidisca*	Thailand, Satun Prov., Baan Suan Tondin (**8**)	ZMMU-A-8145		PQ268503	this work
57	*Kaloula latidisca*	Thailand, Suratthani Prov., Khao Sok (**9**)	ZMMU-A-8146		PQ268504	this work
20	*Kaloula baleata* clade 1	Indonesia, Java isl., Jawa Barat (**10**)	TNHC67086	KC822569		Blackburn et al. 2013
21	*Kaloula baleata* clade 1	Indonesia, Bali Prov., Bali isl. (**11**)	JAM3232	KC822570		Blackburn et al. 2013
22	*Kaloula baleata* clade 1	Indonesia, Sumatra, Way Jepara (**12**)	ZMMU A-04412		PQ268507	this work
23	*Kaloula baleata* clade 1	Indonesia, Sumba (**13**)	KUHE32313	AB634629	AB634687	Matsui et al. 2011
24	*Kaloula baleata* clade 1	Philippines, Palawan isl. (**14**)	ACD1303	KC822582		Blackburn et al. 2013
25	*Kaloula baleata* clade 1	Philippines, Palawan isl. (**14**)	ACD1307	KC822583		Blackburn et al. 2013
26	*Kaloula baleata* clade 1	Indonesia, Sulawesi (–)	JAM3573		KY132185	Alexander et al. 2017
27	*Kaloula baleata* clade 1	Indonesia, Sulawesi Tengah Prov., Pulau Batudaka (**15**)	JAM-3853		KC822568	Blackburn et al. 2013
28	*Kaloula baleata* clade 1	Indonesia, Sulawesi Tengah Prov., Donggala (**16**)	LSUMZ-83998		KC822566	Blackburn et al. 2013
29	*Kaloula baleata* clade 1	Indonesia, Sulawesi Utara Prov., Bogani Nani Wartabone NP (**17**)	LSUMZ-83999		KC822567	Blackburn et al. 2013
30	*Kaloula baleata* clade 2	Malaysia (–)	FRIM1066	KC822579		Blackburn et al. 2013
31	*Kaloula baleata* clade 2	Malaysia (–)	DWNP975	KC822580		Blackburn et al. 2013
32	*Kaloula baleata* clade 2	Malaysia, Johor, Pulau Aceh (**18**)	LSUHC5712	KC822577		Blackburn et al. 2013
33	*Kaloula baleata* clade 2	Malaysia, Sabah, Sepilok (**19**)	LSUHC6156	KC822578		Blackburn et al. 2013
35	*Kaloula baleata* clade 2	Malaysia, Sabah, Kinabalu (**20**)	ZMHA10028		GU154880	Das and Haas 2010
34	*Kaloula baleata* clade 2	Malaysia, Sarawak, Kuching (**21**)	ID8317	KC822581		Blackburn et al. 2013
36	*Kaloula baleata* clade 2	Malaysia, Pahang, Taman Negara (**22**)	ZMMU-A-6152		PQ268508	this work
37	*Kaloula baleata* clade 2	Malaysia, Pahang, Taman Negara (**22**)	ZMMU-A-6153		PQ268509	this work
38	*Kaloula baleata* clade 2	Indonesia, Java, Bogor (**23**)	released (Java)		PQ268505	this work
39	*Kaloula baleata* clade 2	Indonesia, Java, Bogor (**23**)	released (Java)		PQ268506	this work
40	*Kaloula baleata* clade 3	Myanmar, Tanintharyi Div., Yeybu (**24**)	USNM-587865		MT608909	Mulcahy et al. unpublished
41	*Kaloula baleata* clade 3	Myanmar, Tanintharyi Div., Yeybu (**24**)	USNM-587869		MT608910	Mulcahy et al. unpublished
42	*Kaloula baleata* clade 3	Myanmar, Tanintharyi Div., Yeybu (**24**)	USNM-587870		MT608911	Mulcahy et al. unpublished
43	*Kaloula baleata* clade 3	Myanmar, Tanintharyi Div., Yeybu (**24**)	USNM-587871		MT608912	Mulcahy et al. unpublished
44	*Kaloula baleata* clade 3	Myanmar, Tanintharyi Div., Yeybu (**24**)	USNM-587602		MT608913	Mulcahy et al. unpublished
45	*Kaloula baleata* clade 3	Myanmar, Tanintharyi Div., Yeybu (**24**)	USNM-587603		MT608914	Mulcahy et al. unpublished
46	*Kaloula baleata* clade 3	Myanmar, Tanintharyi Div., Yeybu (**24**)	USNM-587863		MT608915	Mulcahy et al. unpublished
47	*Kaloula baleata* clade 3	Myanmar, Tanintharyi Div., Yeybu (**24**)	USNM-587864		MT608916	Mulcahy et al. unpublished
48	*Kaloula baleata* clade 3	Myanmar, Tanintharyi Div., Yeybu (**24**)	USNM-587866		MT608917	Mulcahy et al. unpublished

No.	Species	Locality	Museum / Sample ID	Accession numbers		Reference
	Ingroup			**12S rRNA**	**16S rRNA**	
49	*Kaloula baleata* clade 3	Myanmar, Tanintharyi Div., Yeybu (**24**)	USNM-587867		MT608918	Mulcahy et al. unpublished
50	*Kaloula baleata* clade 3	Myanmar, Tanintharyi Div., Yeybu (**24**)	USNM-587868		MT608919	Mulcahy et al. unpublished
51	*Kaloula baleata* clade 3	Myanmar, Tanintharyi Div., Yeybu (**24**)	USNM-587604		MT608920	Mulcahy et al. unpublished
52	*Kaloula baleata* clade 3	Myanmar, Tanintharyi Div., Yeybu (**24**)	USNM-587861		MT608921	Mulcahy et al. unpublished
53	*Kaloula baleata* clade 3	Myanmar, Tanintharyi Div., Yeybu (**24**)	USNM-587862		MT608922	Mulcahy et al. unpublished
54	*Kaloula baleata* clade 3	Myanmar, Tanintharyi Div., Yeybu (**24**)	USNM-586944		MG935845	Mulcahy et al. 2018
Other *Kaloula* species						
58	*Kaloula borealis*	South Korea, Jeju isl.	KUHE-33139		AB634688	Matsui et al. 2011
59	*Kaloula borealis*	South Korea, Jeju isl.	NIBRAM-000123		JQ815297	Jeong et al. 2013
60	*Kaloula borealis*	South Korea, Jeju isl.	NIBRAM-100348		JQ815298	Jeong et al. 2013
61	*Kaloula borealis*	–	-	JQ692869		Hwang and Lee, 2012
62	*Kaloula borealis*	China, Beijing, Xiangshan	KIZHERP-0173		JX678908	Li et al. 2012
63	*Kaloula borealis*	China, Beijing, Xiangshan	KIZHERP-0174		JX678909	Li et al. 2012
64	*Kaloula conjuncta*	Philippines, Negros isl.	RMB 2252, PNM / CMNH	AY326064		Darst and Canatella, 2003
65	*Kaloula conjuncta*	Philippines, Luzon isl., Palola	ACD 769	KC822537		Blackburn et al. 2013
66	*Kaloula conjuncta*	Philippines, Mindanao isl., Bukidnon Prov.	ACD 996	KC822536		Blackburn et al. 2013
67	*Kaloula conjuncta*	Philippines, Semirara isl., Antique Prov.	KU301849	KC822532		Blackburn et al. 2013
68	*Kaloula conjuncta*	Philippines, Semirara isl., Antique Prov.	KU301854	KC822533		Blackburn et al. 2013
69	*Kaloula conjuncta*	Philippines, Polillo isl., Quezon Prov.	KU303279	KC822527		Blackburn et al. 2013
70	*Kaloula conjuncta*	Philippines, Luzon isl., Laguna Prov.	KU320031	KC822538		Blackburn et al. 2013
71	*Kaloula conjuncta*	Philippines, Mindoro isl., Mindoro Occidental Prov.	KU323280	KC822535		Blackburn et al. 2013
72	*Kaloula conjuncta*	Philippines, Mindoro isl., Mindoro Oriental Prov.	RMB509	KC822534		Blackburn et al. 2013
73	*Kaloula conjuncta*	Philippines, Luzon isl., Quezon Prov.	TNHC59628	KC822539		Blackburn et al. 2013
74	*Kaloula conjuncta*	Philippines, Luzon isl., Albay Prov.	TNHC62972	KC822528		Blackburn et al. 2013
75	*Kaloula conjuncta*	Philippines, Luzon isl., Albay Prov.	TNHC62973	KC822526		Blackburn et al. 2013
76	*Kaloula conjuncta*	Philippines, Luzon isl., Albay Prov.	TNHC62975	KC822530		Blackburn et al. 2013
77	*Kaloula conjuncta*	Philippines, Luzon isl., Albay Prov.	TNHC62976	KC822529		Blackburn et al. 2013
78	*Kaloula conjuncta*	Philippines, Luzon isl., Albay Prov.	TNHC62986	KC822531		Blackburn et al. 2013
79	*Kaloula conjuncta*	Philippines, Camigun Sur isl., Camiguin Sur Prov.	KU309658	KC822588		Blackburn et al. 2013
80	*Kaloula conjuncta*	Philippines, Mindanao isl., Davao del Sur Prov.	TNHC59632	KC822521		Blackburn et al. 2013
81	*Kaloula conjuncta*	Philippines, Mindanao isl., Davao del Sur Prov.	TNHC59635	KC822520		Blackburn et al. 2013
82	*Kaloula conjuncta*	Philippines, Mindanao isl., Davao del Sur Prov.	TNHC59636	KC822522		Blackburn et al. 2013
83	*Kaloula conjuncta*	Philippines, Mindanao isl., Davao del Sur Prov.	TNHC59669	KC822524		Blackburn et al. 2013
84	*Kaloula conjuncta*	Philippines, Mindanao isl., Davao del Sur Prov.	TNHC59670	KC822523		Blackburn et al. 2013
85	*Kaloula conjuncta*	Philippines, Mindanao isl., Davao City Prov.	TNHC59870	KC822525		Blackburn et al. 2013
86	*Kaloula conjuncta*	Philippines, Negros isl., Negros Oriental Prov.	KU328639	KC822518		Blackburn et al. 2013
87	*Kaloula conjuncta*	Philippines, Negros isl., Negros Oriental Prov.	KU328640	KC822519		Blackburn et al. 2013
88	*Kaloula kalingensis*	Philippines, Palaui isl., Cagayan Prov.	KU328643	KC822603		Blackburn et al. 2013
89	*Kaloula kalingensis*	Philippines, Palaui isl., Cagayan Prov.	KU328644	KC822604		Blackburn et al. 2013
90	*Kaloula kalingensis*	Philippines, Luzon isl., Kalinga Prov.	TNHC60118	KC822605		Blackburn et al. 2013
91	*Kaloula kalingensis*	Philippines, Luzon isl., Kalinga Prov.	RMB2210	KC822608		Blackburn et al. 2013
92	*Kaloula kalingensis*	Philippines, Luzon isl., Kalinga Prov.	RMB3137	KC822609		Blackburn et al. 2013
93	*Kaloula kalingensis*	Philippines, Luzon isl., Kalinga Prov.	TNHC59647	KC822610		Blackburn et al. 2013
94	*Kaloula kokacii*	Philippines, Luzon isl., Camarines del Norte Prov.	KU313824	KC822596		Blackburn et al. 2013
95	*Kaloula kokacii*	Philippines, Luzon isl., Camarines Sur Prov.	KU328629	KC822595		Blackburn et al. 2013
96	*Kaloula kokacii*	Philippines, Luzon isl., Albay Prov.	KU328630	KC822590		Blackburn et al. 2013
97	*Kaloula kokacii*	Philippines, Luzon isl., Quezon Prov.	KU328634	KC822593		Blackburn et al. 2013
98	*Kaloula kokacii*	Philippines, Luzon isl., Camarines Sur Prov.	TNHC62684	KC822594		Blackburn et al. 2013
99	*Kaloula kokacii*	Philippines, Luzon isl., Albay Prov.	TNHC62685	KC822589		Blackburn et al. 2013
100	*Kaloula kokacii*	Philippines, Luzon isl., Albay Prov.	TNHC62687	KC822591		Blackburn et al. 2013
101	*Kaloula kokacii*	Philippines, Luzon isl., Sorsogon Prov.	TNHC62688	KC822592		Blackburn et al. 2013
102	*Kaloula mediolineata*	Thailand, Tak Prov.	KUHE35178	AB634631	AB634689	Matsui et al. 2011
103	*Kaloula mediolineata*	Vietnam, Gia Lai Prov.	ROM32838	KC822571		Blackburn et al. 2013
104	*Kaloula mediolineata*	Thailand, Nakhorn Ratchasima Prov.	KU328285	KC822508		Blackburn et al. 2013
105	*Kaloula mediolineata*	Thailand, Nakhorn Ratchasima Prov.	KU328280	KC822509		Blackburn et al. 2013

No.	Species	Locality	Museum / Sample ID	Accession numbers		Reference
	Ingroup			12S rRNA	16S rRNA	
106	*Kaloula mediolineata*	Thailand, Ubon Ratchatani	FMNH265819	KC822510		Blackburn et al. 2013
107	*Kaloula nonggangensis*	China, Guanxi Prov., Nonggang	NHMG-1106040		KC567231	Chen et al. 2013
108	*Kaloula nonggangensis*	China, Guanxi Prov., Nonggang	NHMG-1108035		KC567232	Chen et al. 2013
109	*Kaloula nonggangensis*	China, Guanxi Prov., Nonggang	NHMG-1108036		KC567233	Chen et al. 2013
110	*Kaloula nonggangensis*	China, Guanxi Prov., Nonggang	NHMG-CHN-T20120901		KC567234	Chen et al. 2013
111	*Kaloula picta*	–	KUHE UN	AB634686		Matsui et al. 2011
112	*Kaloula picta*	–	USFS56931		KC180019	de Sa et al. 2012
113	*Kaloula picta*	Philippines, Luzon isl., Cavite Prov.	DLSUD021	KP298039		Brown et al. 2015
114	*Kaloula picta*	Philippines, Palawan isl., Palawan Prov.	ACD1206	KC822541		Blackburn et al. 2013
115	*Kaloula picta*	Philippines, Leyte isl., Leyte Prov.	ACD1242	KC822563		Blackburn et al. 2013
116	*Kaloula picta*	Philippines, Palawan isl., Palawan Prov.	ACD1261	KC822542		Blackburn et al. 2013
117	*Kaloula picta*	Philippines, Palawan isl., Palawan Prov.	ACD1304	KC822540		Blackburn et al. 2013
118	*Kaloula picta*	Philippines, Luzon isl., Pampanga Prov.	ACD1390	KC822546		Blackburn et al. 2013
119	*Kaloula picta*	Philippines, Leyte isl., Leyte Prov.	ACD1501	KC822562		Blackburn et al. 2013
120	*Kaloula picta*	Philippines, Luzon isl., Cavite Prov.	DLSUD020	KC822552		Blackburn et al. 2013
121	*Kaloula picta*	Philippines, Camiguin Sur Isl., Camiguin Sur Prov.	KU301873	KC822565		Blackburn et al. 2013
122	*Kaloula picta*	Philippines, Luzon isl., Laguna Prov.	KU326261	KC822554		Blackburn et al. 2013
123	*Kaloula picta*	Philippines, Luzon isl., Laguna Prov.	KU326262	KC822555		Blackburn et al. 2013
124	*Kaloula picta*	Philippines, Luzon isl., Quezon Prov.	KU326265	KC822548		Blackburn et al. 2013
125	*Kaloula picta*	Philippines, Luzon isl., Cagayan Prov.	RMB4223	KC822551		Blackburn et al. 2013
126	*Kaloula picta*	Philippines, Luzon isl., Cagayan Prov.	RMB4224	KC822550		Blackburn et al. 2013
127	*Kaloula picta*	Philippines, Leyte isl., Leyte Prov.	RMB4294	KC822564		Blackburn et al. 2013
128	*Kaloula picta*	Philippines, Leyte isl., Leyte Prov.	RMB4344	KC822561		Blackburn et al. 2013
129	*Kaloula picta*	Philippines, Bohol isl., Bohol Prov.	TNHC56430	KC822559		Blackburn et al. 2013
130	*Kaloula picta*	Philippines, Bohol isl., Bohol Prov.	TNHC56431	KC822560		Blackburn et al. 2013
131	*Kaloula picta*	Philippines, Cebu isl., Cebu Prov.	TNHC56468	KC822543		Blackburn et al. 2013
132	*Kaloula picta*	Philippines, Mindanao isl., Davao del Sur Prov.	TNHC59653	KC822558		Blackburn et al. 2013
133	*Kaloula picta*	Philippines, Mindanao isl., Davao del Sur Prov.	TNHC59654	KC822557		Blackburn et al. 2013
134	*Kaloula picta*	Philippines, Mindanao isl., Davao del Sur Prov.	TNHC59871	KC822556		Blackburn et al. 2013
135	*Kaloula picta*	Philippines, Luzon isl., Albay Prov.	TNHC62470	KC822549		Blackburn et al. 2013
136	*Kaloula picta*	Philippines, Luzon isl., Zambales Prov.	TNHC62471	KC822547		Blackburn et al. 2013
137	*Kaloula picta*	Philippines, Polillo isl., Quezon Prov.	USNM-FS56932	KC822545		Blackburn et al. 2013
138	*Kaloula picta*	Philippines, Polillo isl., Quezon Prov.	USNM-FS-56936	KC822544		Blackburn et al. 2013
139	*Kaloula pulchra*	Thailand, Nong Khai	KUHE 22206	AB634632	AB634690	Matsui et al. 2011
140	*Kaloula pulchra*	Thailand, Kanchanaburi, Thong Pha Phum	KUHE 35171	AB201183	AB201194	Matsui et al. 2005
141	*Kaloula pulchra*	Myanmar, Sagaing	USFS34083		KC180025	de Sa et al. 2012
142	*Kaloula pulchra*	Vietnam, Cat Ba	ZMMU-A-4761-1		PQ268519	this work
143	*Kaloula pulchra*	Vietnam, Cat Ba	ZMMU-A-4761-2		PQ268520	this work
144	*Kaloula pulchra*	Bangladesh, Sylhet	IABHU-3781 / Kpul-Bd1		AB530543	Hasan et al. 2012
145	*Kaloula pulchra*	Bangladesh, Bandarban	IABHU 3783 / Kpul-Bd2		AB530544	Hasan et al. 2012
146	*Kaloula pulchra*	Myanmar	KIZHERP0439		JX678910	Li et al. 2012
147	*Kaloula pulchra*	Thailand, Ranong	-		AB530633	Hasan et al. 2014
148	*Kaloula pulchra*	Indonesia, Sulawesi, Makassar	-		AB530639	Hasan et al. 2014
149	*Kaloula pulchra*	Malaysia	VUB0677		EF017955	Van Bocxlaer et al. 2006
150	*Kaloula pulchra*	–	-	NC006405		Zhang et al. 2005
151	*Kaloula pulchra*	Myanmar	KIZHERP3003		JX678902	Li et al. 2012
152	*Kaloula pulchra*	China, Yunnan, Jinghong	KIZHERP0121		JX678903	Li et al. 2012
153	*Kaloula pulchra*	China, Yunnan, Mengla	KIZHERP0129		JX678904	Li et al. 2012
154	*Kaloula pulchra*	China, Guangxi, Qinzhou	KIZHERP0171		JX678907	Li et al. 2012
155	*Kaloula pulchra*	Thailand, Phang Nga	P994		KR827832	Grosjean et al. 2015
156	*Kaloula pulchra*	China, Hainan	GRE119/G027		KR827833	Grosjean et al. 2015
157	*Kaloula pulchra*	Myanmar, Tanintharyi	USNM:Herp:586945		MG935846	Mulcahy et al. 2018
158	*Kaloula pulchra*	Myanmar, Tanintharyi	USNM:Herp:586946		MG935847	Mulcahy et al. 2018
159	*Kaloula pulchra*	Myanmar, Sagaing	USNM:Herp:520322		MG935848	Mulcahy et al. 2018
160	*Kaloula pulchra*	Myanmar, Sagaing	USNM:Herp:520326		MG935849	Mulcahy et al. 2018
161	*Kaloula pulchra*	Myanmar, Bago	MBM-USNMFS35512		MG935850	Mulcahy et al. 2018

No.	Species	Locality	Museum / Sample ID	Accession numbers		Reference
	Ingroup			12S rRNA	16S rRNA	
162	*Kaloula pulchra*	Myanmar, Yangon	MBM-JBS19849		MG935851	Mulcahy et al. 2018
163	*Kaloula pulchra*	Myanmar, Sagaing	USNM:Herp:523967		MG935852	Mulcahy et al. 2018
164	*Kaloula pulchra*	Myanmar, Mandalay	MBM-USNMFS36482		MG935853	Mulcahy et al. 2018
165	*Kaloula pulchra*	China, Guangxi, Nonggang	NHMG<CHN>:1106008		KC567235	Mo et al. 2013
166	*Kaloula pulchra*	China, Guangxi, Nonggang	NHMG<CHN>:1106009		KC567236	Mo et al. 2013
167	*Kaloula pulchra*	China	-		AF315162	Jiang and Zhou., 2001
168	*Kaloula pulchra*	Southeast Asia	ZCYK-Kpul1		LC640532	Kambayashi et al. 2022
169	*Kaloula pulchra*	Bangladesh	-		MN477194	Rony et al. unpublished
170	*Kaloula pulchra*	Vietnam, Ha Tinh Prov., Huong Son	AMCC 106697	DQ283397		Frost et al. 2005
171	*Kaloula pulchra*	pet trade	RdS 02	DQ283398		Frost et al. 2005
172	*Kaloula pulchra*	–	SIH-09		AY330893	Hoegg et al. 2004
173	*Kaloula pulchra*	Thailand	ACD1538	KC822621		Blackburn et al. 2013
174	*Kaloula pulchra*	Laos, Khammouane Prov., Boudalapha	FMNH225128	KC822620		Blackburn et al. 2013
175	*Kaloula pulchra*	Laos, Bolikhamxay Prov., Thaphabat	FMNH225129	KC822619		Blackburn et al. 2013
176	*Kaloula pulchra*	Malaysia, Selangor Prov.	JAM1753	KC822616		Blackburn et al. 2013
177	*Kaloula pulchra*	Malaysia, Pahang Prov., Tioman isl.	JAM1857	KC822615		Blackburn et al. 2013
178	*Kaloula pulchra*	Malaysia, Pahang, Pulau Tioman	LSUHC3869	KC822575		Blackburn et al. 2013
179	*Kaloula pulchra*	Malaysia (continental)	LSUHC3870	KC852906		Blackburn et al. 2013
180	*Kaloula pulchra*	Indonesia, Sumatra isl.	MF0766	KC822623		Blackburn et al. 2013
181	*Kaloula pulchra*	Indonesia, Sumatra isl.	MF0812	KC822624		Blackburn et al. 2013
182	*Kaloula pulchra*	China	NHMS3208	KC822614		Blackburn et al. 2013
183	*Kaloula pulchra*	Indonesia, Sulawesi isl., Propinsi Sulawesi Selatan	TNHC59422	KC822618		Blackburn et al. 2013
184	*Kaloula pulchra*	Indonesia, Sulawesi isl., Propinsi Sulawesi Selatan	TNHC59423	KC822617		Blackburn et al. 2013
185	*Kaloula pulchra*	Vietnam	TZ629	KC822622		Blackburn et al. 2013
186	*Kaloula pulchra*	China	-		AF315130	Jiang and Zhou., 2001
187	*Kaloula rigida*	Philippines, Luzon isl., Benguet Prov.	ACD1570	KC822636		Blackburn et al. 2013
188	*Kaloula rigida*	Philippines, Luzon isl., Isabela Prov., San Mariano	ACD1954	KC822631		Blackburn et al. 2013
189	*Kaloula rigida*	Philippines, Luzon isl., Isabela Prov., San Mariano	ACD2043	KC822632		Blackburn et al. 2013
190	*Kaloula rigida*	Philippines, Luzon isl., Isabela Prov., San Mariano	ACD2044	KC822634		Blackburn et al. 2013
191	*Kaloula rigida*	Philippines, Luzon isl., Kalinga Prov.	ACD2032	KC822633		Blackburn et al. 2013
192	*Kaloula rigida*	Philippines, Luzon isl., Sierra Madres	ACD660	KC822626		Blackburn et al. 2013
193	*Kaloula rigida*	Philippines, Luzon isl., Kalinga Prov., Balbalan	ACD756	KC822628		Blackburn et al. 2013
194	*Kaloula rigida*	Philippines, Luzon isl., Isabela Prov., San Mariano	KU326470	KC822635		Blackburn et al. 2013
195	*Kaloula rigida*	Philippines, Luzon isl., Cagayan Prov., Pagudpud	KU328628	KC822627		Blackburn et al. 2013
196	*Kaloula rigida*	Philippines, Luzon isl., Cagayan Prov., Gattaran	RMB4226	KC822625		Blackburn et al. 2013
197	*Kaloula rigida*	Philippines, Luzon isl., Kalinga Prov., Balbalan	TNHC59644	KC822629		Blackburn et al. 2013
198	*Kaloula rigida*	Philippines, Luzon isl., Kalinga Prov., Balbalan	TNHC60119	KC822630		Blackburn et al. 2013
199	*Kaloula rugifera*	China, Sichuan, Mianyang	KIZHERP071601		JX678911	Li et al. 2012
200	*Kaloula rugifera*	China, Sichuan, Mianyang	KIZHERP071602		JX678912	Li et al. 2012
201	*Kaloula rugifera*	China, Sichuan, Mianyang	CIB20110802028		KC567237	Mo et al. 2013
202	*Kaloula verrucosa*	China, Sichuan, Huidong	CIB20090349		KC567238	Mo et al. 2013
203	*Kaloula verrucosa*	China, Sichuan, Huidong	CIB20090351		KC567239	Mo et al. 2013
204	*Kaloula verrucosa*	China, Yunnan, Chuxiong	KIZHERP2015		JX678900	Li et al. 2012
205	*Kaloula verrucosa*	China, Yunnan, Wuliangshan	KIZHERP2020		JX678901	Li et al. 2012
206	*Kaloula verrucosa*	China	NMNS 3246	KC822507		Blackburn et al. 2013
207	*Kaloula walteri*	Philippines, Mindanao isl., Bukidnon Prov., Malagaylay	ACD994	KC822640		Blackburn et al. 2013
208	*Kaloula walteri*	Philippines, Polillo isl., Quezon Prov., Polillo	KU303285	KC822642		Blackburn et al. 2013
209	*Kaloula walteri*	Philippines, Luzon isl., Quezon Prov., Lucban	KU327338	KC822639		Blackburn et al. 2013
210	*Kaloula walteri*	Philippines, Luzon isl., Quezon Prov., Tayabas	RMB3701	KC822641		Blackburn et al. 2013
211	*Kaloula walteri*	Philippines, Luzon isl., Quezon Prov., Lucban	TNHC59667	KC822637		Blackburn et al. 2013
212	*Kaloula walteri*	Philippines, Luzon isl., Quezon Prov., Lucban	TNHC60116	KC822638		Blackburn et al. 2013
213	*Kaloula* sp.	Philippines, Luzon isl., Laguna Prov.	ACD1692	KC822602		Blackburn et al. 2013
214	*Kaloula* sp.	Philippines, Luzon isl., Sierra Madres	ACD2479	KC822606		Blackburn et al. 2013
215	*Kaloula* sp.	Philippines, Luzon isl., Isabela Prov., Palanan	ACD650	KC822607		Blackburn et al. 2013
216	*Kaloula* sp.	Philippines, Luzon isl., Laguna Prov., Los Banos	ACD943	KC822597		Blackburn et al. 2013
217	*Kaloula* sp.	Philippines, Luzon isl., Laguna Prov., Los Banos	ACD945	KC822598		Blackburn et al. 2013

No.	Species	Locality	Museum / Sample ID	Accession numbers		Reference
	Ingroup			12S rRNA	16S rRNA	
218	*Kaloula* sp.	Philippines, Luzon isl., Laguna Prov., Los Banos	FMNH267555	KC822599		Blackburn et al. 2013
219	*Kaloula* sp.	Philippines, Luzon isl., Aurora Prov., Aurora Memorial NP	RMB750	KC822601		Blackburn et al. 2013
220	*Kaloula* sp.	Philippines, Luzon isl., Aurora Prov., Aurora Memorial NP	RMB783	KC822600		Blackburn et al. 2013
221	*Kaloula* sp.	Philippines, Panay isl., Antique Prov., Sibalom	GVAG253	KC822515		Blackburn et al. 2013
222	*Kaloula* sp.	Philippines, Panay isl., Antique Prov., Sibalom	GVAG255	KC822514		Blackburn et al. 2013
223	*Kaloula* sp.	Philippines, Sibuyan isl., Rombolon Prov.	KU328607	KC822511		Blackburn et al. 2013
224	*Kaloula* sp.	Philippines, Sibuyan isl., Rombolon Prov.	KU328608	KC822512		Blackburn et al. 2013
225	*Kaloula* sp.	Philippines, Panay isl., Antique Prov.	MG012	KC822513		Blackburn et al. 2013
226	*Kaloula* sp.	Philippines, Panay isl., Antique Prov.	TNHC56341	KC822516		Blackburn et al. 2013
227	*Kaloula* sp.	Philippines, Panay isl., Antique Prov.	TNHC56343	KC822517		Blackburn et al. 2013
228	*Kaloula* sp.	Philippines, Samar isl., Eastern Samar Prov., Taft	KU310699	KC822587		Blackburn et al. 2013
229	*Kaloula* sp.	Philippines, Leyte isl., Leyte Prov., Danao	KU328632	KC822584		Blackburn et al. 2013
230	*Kaloula* sp.	Philippines, Leyte isl., Leyte Prov., Danao	KU328633	KC822585		Blackburn et al. 2013
231	*Kaloula* sp.	Philippines, Leyte isl., Leyte Prov., Baybay	KU328645	KC822586		Blackburn et al. 2013
232	*Kaloula* sp.	Philippines, Panay isl., Antique Prov., Sibalom	MG0000	KC822611		Blackburn et al. 2013
233	*Kaloula* sp.	Philippines, Panay isl., Antique Prov., Sibalom	MG0001	KC822612		Blackburn et al. 2013
234	*Kaloula* sp.	Philippines, Panay isl., Antique Prov., Sibalom	MG0002	KC822613		Blackburn et al. 2013
	Outgroups					
235	*Uperodon taprobanicus*	Bandgladesh, Mymensingh	Ktap-Bd		AB530545	Hasan et al. 2012
236	*Uperodon taprobanicus*	Sri Lanka	KUHE-37252	AB634633	AB634691	Matsui et al. 2011
237	*Uperodon taprobanicus*	–	-		AY948729	Roelants et al. 2007
238	*Kalophrynus interlineatus*	–	KIZ-HERP-0169		JX678906	Li et al. 2012

These characters were measured in specimens from Khammouane Province, Laos, and Dong Nai and Lam Dong provinces, Vietnam, as well as specimens of *K. indochinensis* from the type locality (Gia Lai Province, central Vietnam). We performed a Principal Component Analysis (PCA) in Statistica v10.0 (StatSoft, Inc. 2011) to examine overall morphological variation among the populations of *K. indochinensis* sensu stricto and the populations of *Kaloula* spp. from central Laos and southern Vietnam. We conducted PCA using SVL and size-corrected values for characters 2–23 (their ratios to SVL), following the methodology of Nishikawa et al. (2007). The first two principal components (i.e., those that explained the highest proportion of variance) were extracted for display with an ordination plot.

Furthermore, we compare external morphological characters based on information taken from the literature (e.g., Chan et al. 2013, 2014; Mo et al. 2013).

Bioacoustic analysis

Male advertisement calls of *Kaloula* sp. were recorded in Cat Tien National Park, near Nam Cat Tien Village, Tan Phu District, Dong Nai Province, Vietnam, on August 4, 2023 (11.410618°N, 107.419334°E; altitude 119 m a.s.l.); the record was taken at an air temperature of 24.0 °C. Male advertisement calls (described as calls hereafter) were recorded with an Apple iPhone X (iPhone 10); the calls were recorded at a distance of approximately 0.1–0.2 m from the calling males; an HTC-2 Digital LCD Thermometer Hygrometer with an outdoor sensor attached was used to take ambient temperatures and humidity at the calling site after the recording. The software Raven Pro 1.6 (http://www.birds.cornell.edu/raven) was used to analyze the recorded calls. Audio spectrograms were calculated with a fast Fourier transform (FFT) of 512 points, 90% overlap, and 135 Hz grid spacing using the Hanning window. The terminology of call analysis and description using a call-centered approach (defining uninterrupted units as calls whenever they are separated by long silent intervals) follows Koehler et al. (2017). We examined oscillograms (waveforms) and audio spectrograms of vocalizations and measured the call duration (in milliseconds—ms), intercall interval duration (ms), call repetition rate (calls/s and calls/min), number of notes per call (notes/call), harmonic frequency (kHz), and dominant frequency (kHz). We qualitatively compared the call of *Kaloula* sp. from Cat Tien National Park with the call parameters of *K. indochinensis* sensu stricto from Gia Lai Province, Vietnam, given by Nguyen et al. (2022).

Results

Genealogical mitochondrial relationships

The trees recovered by the BI and ML analyses featured essentially similar topologies, with the only differences being the relationships between the higher *K. baleata* clades. Our mtDNA-genealogy confirms the monophyly of the genus *Kaloula* (0.98/96; hereafter node support values are given for BIPP/UFB, respectively) with respect to its sister genus *Uperodon* Duméril & Bibron, 1841 (Fig. 2). Relationships between different groups

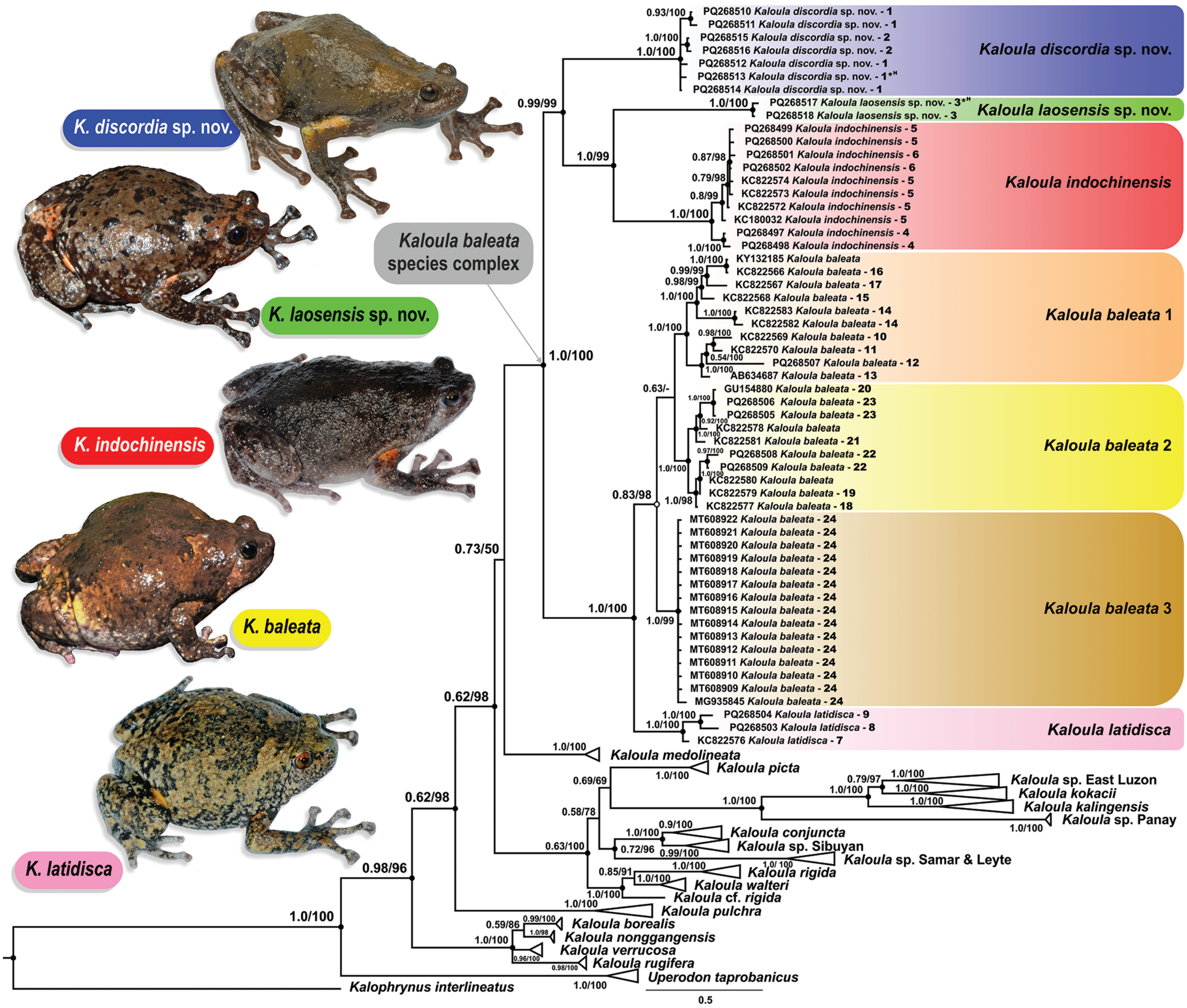

Figure 2. Genealogical relationships of the genus *Kaloula* based on the analysis of mtDNA fragments, including 12S rRNA, tRNAVal, and 16S rRNA gene sequences. Numbers at tree nodes correspond to PP/UFB support values, respectively. Black circles correspond to well-supported (PP ≥ 0.95 or UFB ≥ 90) nodes. Numbers in bold following sample names correspond to localities in Fig. 1 and Table 1. The information on GenBank Accession Numbers, museum vouchers, and localities of origin for sequences used in this study is summarized in Table 1. The holotypes of *Kaloula discordia* sp. nov. and *Kaloula laosensis* sp. nov. are marked with asterisks (*H). Photographs by N.A. Poyarkov and N.L. Orlov.

within *Kaloula*, however, were not statistically supported. The East Asian diversification of *Kaloula*, including *K. borealis* (Barbour, 1908), *K. nonggangensis*, *K. verrucosa* Boulenger, 1904, and *K. rugifera* Stejneger, 1924 (1.0/100), is suggested as a sister group with respect to all other *Kaloula* species, but this topology got strong support only in the ML analysis (0.62/98). *Kaloula pulchra* Gray, 1831, is recovered as a sister species to all remaining species of *Kaloula*, again without significant nodal support by BI PP (0.62/98). All the remaining *Kaloula* species are grouped in three major clades, with their respective branching being unresolved (0.73/50): (1) the *K. baleata* species complex; (2) *K. mediolineata* Smith, 1917; (3) the *Kaloula* species found across the Southeast Asian Islands. In the latter, populations from the Philippine Archipelago and adjacent Southeast Asian islands, including *K. picta* (Duméril & Bibron, 1841), *K. kalingensis* Taylor, 1922, *K. kokacii* Ross & Gonzales, 1992, *K. conjuncta* (Peters, 1863), *K. rigida* Taylor, 1922, *K. walteri* Diesmos, Brown & Alcala, 2002, together with unnamed candidate species (noted sp.), are grouped in a clade, again with little support by BI PP (0.63/100). *Kaloula rigida* is paraphyletic with respect to *K. walteri* in the 12S-16S tree. The sister species of the *K. baleata* species complex is given as *K. mediolineata*, again with little support (0.73/50). The *K. baleata* species complex is monophyletic (1.0/100) and features two major clades (Fig. 2): (1) One clade is composed of *K. latidisca* from Peninsular Malaysia and southern Thailand (1.0/100), together with three divergent lineages of *K. baleata* sensu lato (1.0/100) from the Sunda Islands, Sulawesi, Palawan, and southern Myanmar; (2) the second clade (0.99/99) comprises populations from eastern Indochina, including two unnamed candidate species (labelled *Kaloula* sp.),

one from southern Vietnam (1.0/100) and one from central Laos (1.0/100), the latter being most closely related to *K. indochinensis* from central Vietnam (1.0/100).

Kaloula baleata sensu lato, which monophyly is robustly supported only in the ML analysis (0.83/98), features three geographically circumscribed mitochondrial lineages (see Fig. 2): (1) *K. baleata* 1 is distributed in Palawan Island of the Philippines and Sulawesi, Sumba, Bali, central Java, and southern Sumatra Islands of Indonesia; (2) *K. baleata* 2 is distributed in Sarawak and Sabah in Borneo and eastern Peninsular Malaysia, including the island of Tioman, as well as western Java, in sympatry with *K. baleata* 1; (3) *K. baleata* 3 is confirmed from a single locality in Tanintharyi Region, southern Myanmar (see Fig. 1).

Mitochondrial distances

The uncorrected genetic *p*-distances for the 16S rRNA gene fragment among members of the genus *Kaloula* are available in Table 2. Interspecific distances among *Kaloula* species varied from 1.43% (between *K. verrucosa* and *K. nonggangensis*) to 14.62% (between *K. rugifera* and an undescribed species, *Kaloula* sp. from Panay, Philippines). Intraspecific distances were high in several currently recognized species, including *K. kokacii* (up to 3.39%), but especially in *K. indochinensis* from the *K. baleata* complex, where populations from Khammouane Province, Laos, as well as from Dong Nai and Lam Dong provinces, Vietnam, showed *p*-distances from the closest taxon above 4.45% and 4.33%, respectively. These 16S distances are much higher than the proposed threshold of 3% for species-level divergence in anurans (Vieites et al. 2009), which was also recently supported to delimit species based on instances of reproductive isolation (Dufresnes et al. 2021). Accordingly, these distances are higher than the *p*-distances observed between some sister species pairs in the *K. baleata* complex, namely 3.0% between *K. baleata* and *K. latidisca*. We also report a high interspecific variation in *K. baleata*, namely 2.72% between *K. baleata* 1 and *K. baleata* 2.

Morphology

Given the limited number of morphometric characters provided in the original description of *K. indochinensis* in Chan et al. (2013), we did not incorporate their data in our analysis, which further avoids measurer bias. Consequently, the morphological data on *K. indochinensis* relies only on our specimens from near the type locality of this species in Kon Ka Kinh National Park in Gia Lai Province, central Vietnam, as well as in Yok Don National Park in Dak Lak Province, central Vietnam. These specimens were confirmed as *K. indochinensis* by the genetic analysis (Fig. 2). The first two principal components (PCs) of the PCA explain 48.72% (PC1: 28.68%, PC2: 20.04%) of the variation among specimens of *K. indochinensis*, *Kaloula* sp. from central Laos, and *Kaloula* sp. from southern Vietnam (Fig. 3). The specimens of each population/candidate species form distinct groups in the morphospace, without overlapping, and also with respect to sex (Fig. 3).

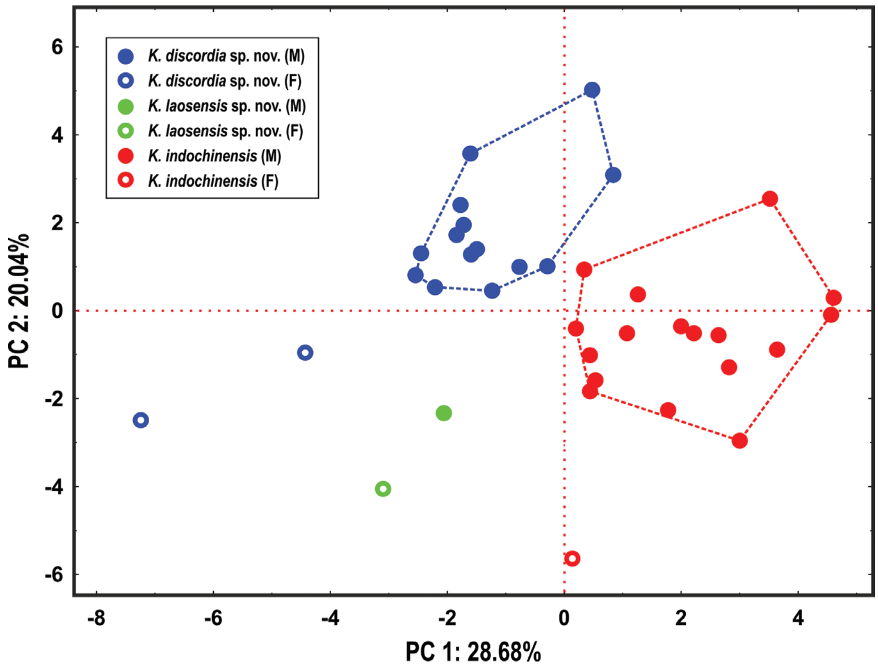

Figure 3. Scatterplot of first two PCs in the principal component analysis (PCA) on morphological data from *Kaloula indochinensis*, *Kaloula discordia* sp. nov. from southern Vietnam, and *Kaloula laosensis* sp. nov. from Khammouane, central Laos, overlayed by convex hull polygons; filled circles indicate male specimens, and empty circles indicate female specimens. The morphological data used in the analysis is presented in Table 3.

Table 2. Uncorrected average interspecific (below and above diagonal) and intraspecific (on the diagonal) genetic *p*-distances for the 16S rRNA mtDNA gene fragment (in percentage) are given for species of the genus *Kaloula*.

	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	*Kaloula discordia* sp. nov.	0.39	4.45	6.17	5.41	5.40	5.47	6.29	4.33	7.00	6.74	9.57	11.17	8.14	6.25	6.98	7.17	6.08	7.45	7.00	6.65	12.77	9.41	10.61	6.54
2	*Kaloula laosensis* sp. nov.	4.45	0.22	4.77	6.81	6.59	7.03	7.09	6.28	7.24	8.14	10.74	12.08	7.93	7.65	8.95	8.47	7.47	6.78	7.01	7.89	14.01	10.69	10.64	8.39
3	*K. indochinensis*	6.17	4.77	0.37	7.24	7.25	6.85	8.20	6.26	7.90	7.45	11.87	12.98	8.37	7.92	8.82	8.70	6.86	6.96	7.29	7.84	15.09	11.44	11.07	7.81
4	*K. baleata* 1	5.41	6.81	7.24	1.37	2.72	2.08	3.22	4.79	6.64	7.07	9.72	10.85	8.05	6.90	6.71	7.37	6.24	8.19	7.21	6.72	12.46	9.26	11.25	7.57
5	*K. baleata* 2	5.40	6.59	7.25	2.72	2.56	2.65	3.96	5.36	6.74	7.29	10.26	11.31	7.92	7.35	7.14	7.74	6.76	8.19	7.04	6.82	12.59	9.67	10.59	7.84
6	*K. baleata* 3	5.47	7.03	6.85	2.08	2.65	0.00	3.00	4.98	6.65	6.44	9.10	10.74	7.57	6.86	6.80	7.06	5.99	7.80	6.51	6.26	13.66	9.00	9.95	7.34
7	*K. latidisca*	6.29	7.09	8.20	3.22	3.96	3.00	1.45	6.04	7.28	7.47	9.71	11.01	8.89	7.41	7.26	7.74	7.13	8.43	7.82	7.24	14.05	9.41	11.83	7.66
8	*K. mediolineata*	4.33	6.28	6.26	4.79	5.36	4.98	6.04	0.55	5.89	5.43	8.74	10.49	6.12	5.70	6.95	6.05	5.61	6.81	5.46	5.39	12.30	8.49	10.02	4.97
9	*K. borealis*	7.00	7.24	7.90	6.64	6.74	6.65	7.28	5.89	0.00	7.43	10.12	11.18	2.07	7.07	7.92	7.46	6.44	2.76	1.93	6.78	13.40	9.91	10.11	7.75
10	*K. conjuncta*	6.74	8.14	7.45	7.07	7.29	6.44	7.47	5.43	7.43	1.39	8.37	9.78	8.18	5.08	8.59	4.56	3.53	7.70	8.00	3.56	11.65	8.05	7.06	2.57
11	*K. kalingensis*	9.57	10.74	11.87	9.72	10.26	9.10	9.71	8.74	10.12	8.37	2.07	6.18	10.05	9.39	11.22	8.23	7.55	9.74	9.43	7.52	10.16	4.43	11.20	7.78
12	*K. kokacii*	11.17	12.08	12.98	10.85	11.31	10.74	11.01	10.49	11.18	9.78	6.18	3.39	11.41	10.64	11.73	9.29	9.26	10.64	10.51	8.25	9.62	4.48	12.17	9.25
13	*K. nonggangensis*	8.14	7.93	8.37	8.05	7.92	7.57	8.89	6.12	2.07	8.18	10.05	11.41	0.00	7.73	8.60	8.77	8.05	2.76	1.43	8.35	14.14	10.02	11.05	8.14
14	*K. picta*	6.25	7.65	7.92	6.90	7.35	6.86	7.41	5.70	7.07	5.08	9.39	10.64	7.73	0.31	9.40	3.83	3.15	7.54	8.18	3.51	11.78	8.75	9.18	4.56
15	*K. pulchra*	6.98	8.95	8.82	6.71	7.14	6.80	7.26	6.95	7.92	8.59	11.22	11.73	8.60	9.40	0.68	8.88	8.98	8.56	7.93	9.27	14.15	10.63	12.93	8.41
16	*K. rigida*	7.17	8.47	8.70	7.37	7.74	7.06	7.74	6.05	7.46	4.56	8.23	9.29	8.77	3.83	8.88	1.90	2.73	8.56	7.99	2.45	9.90	7.82	7.74	3.58
17	*K.* cf. *rigida*	6.08	7.47	6.86	6.24	6.76	5.99	7.13	5.61	6.44	3.53	7.55	9.26	8.05	3.15	8.98	2.73	n/c	7.59	7.45	1.92	10.72	7.78	6.82	3.88
18	*K. rugifera*	7.45	6.78	6.96	8.19	8.19	7.80	8.43	6.81	2.76	7.70	9.74	10.64	2.76	7.54	8.56	8.56	7.59	0.00	1.98	8.12	14.62	9.33	10.70	7.98
19	*K. verrucosa*	7.00	7.01	7.29	7.21	7.04	6.51	7.82	5.46	1.93	8.00	9.43	10.51	1.43	8.18	7.93	7.99	7.45	1.98	0.27	7.48	13.70	9.19	10.44	7.68
20	*K. walteri*	6.65	7.89	7.84	6.72	6.82	6.26	7.24	5.39	6.78	3.56	7.52	8.25	8.35	3.51	9.27	2.45	1.92	8.12	7.48	0.30	9.38	6.72	6.61	3.19
21	*Kaloula* sp. Panay	12.77	14.01	15.09	12.46	12.59	13.66	14.05	12.30	13.40	11.65	10.16	9.62	14.14	11.78	14.15	9.90	10.72	14.62	13.70	9.38	0.00	8.51	12.80	10.47
22	*Kaloula* sp. East Luzon	9.41	10.69	11.44	9.26	9.67	9.00	9.41	8.49	9.91	8.05	4.43	4.48	10.02	8.75	10.63	7.82	7.78	9.33	9.19	6.72	8.51	1.85	10.44	7.51
23	*Kaloula* sp. Samar & Leyte	10.61	10.64	11.07	11.25	10.59	9.95	11.83	10.02	10.11	7.06	11.20	12.17	11.05	9.18	12.93	7.74	6.82	10.70	10.44	6.61	12.80	10.44	1.56	7.78
24	*Kaloula* sp. Sibuyan	6.54	8.39	7.81	7.57	7.84	7.34	7.66	4.97	7.75	2.57	7.78	9.25	8.14	4.56	8.41	3.58	3.88	7.98	7.68	3.19	10.47	7.51	7.78	1.66

Bioacoustics

The advertisement call of *Kaloula* sp. from southern Vietnam is documented based on the recordings of one calling male individual. Males of *Kalophrynus interlineatus* (Blyth, 1855), *Occidozyga martensii* (Peters, 1867), and *Microhyla mukhlesuri* Hasan, Islam, Kuramoto, Kurabayashi & Sumida, 2014, were also calling at the same habitat. The calls of *Kaloula* sp. are slow and low-pitched, resonant, booming sounds that resemble the sound of a bicycle horn to the human ear. Call parameters are shown in Table 3, and the sonograms and waveforms of the call are presented in Fig. 4. The call consists of a single note with 11–13 pulses with an average duration of 190.8 ms (144.8–260.6 ms, N = 23). Calls were repeated at a rate of one call per second, 56.5 (42–71) calls per minute, and had an average intercall interval of 1,222.9 ms (327.1–8,954.4 ms, N = 23). The fundamental frequency was not evident, and the average dominant frequency was 0.30–0.45 kHz. Three harmonics were detected at 1.0, 1.2, and 1.5 kHz (Table 3, Fig. 4). The call of the Laos population of *Kaloula* sp. was not recorded.

Systematics

The two populations of *Kaloula* spp. from Laos and southern Vietnam belong to the *K. baleata* species complex and are characterized by divergent mitochondrial lineages and distinctive morphologies. Their amount of 16S divergence (Table 2), together with the substantial morphological differentiation between them and the closely related species *K. indochinensis* (Fig. 3), suggests a species-level split. Based on our mitochondrial genealogy, the species from Khammouane Province of Laos is the sister species of *K. indochinensis*, while the species from southern Vietnam is the sister species of a clade including *K. indochinensis* and the Laos species (Fig. 2). In addition to diagnostic morphological differences (see below), the three Indochinese species of the *K. baleata* species complex also feature stable differences in coloration, as well as differences in bioacoustic characteristics for the studied Vietnamese species. The distribution of all members of the *K. baleata* species complex in Indochina, following our results, is detailed in Fig. 5. Given the congruence of morphological, bioacoustic, and molecular data in suggesting a deep divergence of the Laos and southern Vietnam *Kaloula* sp. populations from all currently recognized species in the genus, we herein describe them as two new species of *Kaloula*.

Kaloula discordia Poyarkov, Gorin, Bragin & Nguyen, sp. nov.

https://zoobank.org/3E487D92-32B2-447E-AB70-0059D2F504A9

Figs 2, 4, 6–8, 9C, Tables 3, 4

Chresonymy. *Kaloula baleata* [partim]—Orlov et al. (2002: 99); Nguyen et al. (2005: 43); Orlov and Ananjeva (2007: 148); Nguyen et al. (2009: 94).

Kaloula indochinensis [partim]—Chan et al. (2013: 334, 2014: 577); Chandramouli and Prasad (2018: 52); Poyarkov et al. (2021b: 39); Vassilieva (2021: 72–73); Holden (2023: 149).

Holotype. ZMMU A-8134 (field number NAP-14688), adult male, from a pond in Cat Tien National Park, along the road from park headquarters to the Bau Sau Lake, Dong Nai River valley, Dac Lua Commune, Tan Phu District, Dong Nai Province, Vietnam, collected by N.A. Poyarkov, A.M. Bragin, and V.A. Gorin on 15 June, 2024 (11.44121°N, 107.41312°E; elevation 137 m a.s.l.) (Figs 6, 7C).

Paratypes (n = 14). ZMMU A-8135–A-8140 (field numbers NAP-14689–14694), six adult males with collection data same as the holotype; ZMMU A-8141–A-8143 (field numbers NAP-14688–14694), three adult males with collection data same as the holotype; ZISP 15285–15287 (field numbers NAP-14687, NAP-14695–14696), three adult males with collection data same as the holotype; ZMMU A-4739 (field number NAP-01674), adult male from Cat Tien National Park, Dong Nai River valley, Dac Lua Commune, Tan Phu District, Dong Nai Province, Vietnam, collected by N.A. Poyarkov on June 1, 2011 (11.44576°N, 107.38673°E; elevation 128 m a.s.l.); ZMMU A-4642 (field number NAP-00630), adult female from Cat Tien National Park, Dong Nai River valley, Dac Lua Commune, Tan Phu District, Dong Nai Province, Vietnam, collected by N.A. Poyarkov and A.B. Vassilieva on June 2, 2009 (11.44576°N, 107.38673°E; elevation 128 m a.s.l.) (Fig. 8).

Referred materials (n = 3). ZMMU-A-4602-1–3 (field numbers NAP-02010, NAP-02086, and NAP-02122), adult female and two subadult females from Cat Tien National Park, Dong Nai River valley, Dac Lua Commune, Tan Phu District, Dong Nai Province, Vietnam, collected by E.A. Galoyan on August 22, 2011, September 15, 2011, and November 11, 2011 (11.419503°N, 107.426442°E; elevation 117 m a.s.l.).

Diagnosis. *Kaloula discordia* sp. nov. is distinguished from its congeners by the following combination of morphological characters: (1) medium body size (SVL 42.9–56.2 mm); (2) eyes comparatively small (eye length comprising 60%–75% of snout length); (3) dorsally uniform dark olive-brown; (4) beige-gray ventrally with irregular white mottling on belly and limbs; (5) pale yellow or orange-brown 8-shaped patch on either side of the neck posterior to eyes; (6) yellowish to orange axillary patch present; (7) grayish to beige-yellow inguinal patch present edged with black markings; (8) from gray to beige spot on tibiotarsal articulation present; (9) dark interorbital bar absent; (10) enlarged, widened finger disks (3FDD 6.5%–7.5% of SVL), ca. 1.27 times wider than toe disks; (11) finger subarticular tubercle formula: 1:1:2:2; (12) toe subarticular tubercle formula: 1:1:2:2:2; (13) two metacarpal tubercles not in touch with each other; (14) two metatarsal tubercles, outer metatarsal tubercle rounded, smaller than elongated inner metatarsal tubercle.

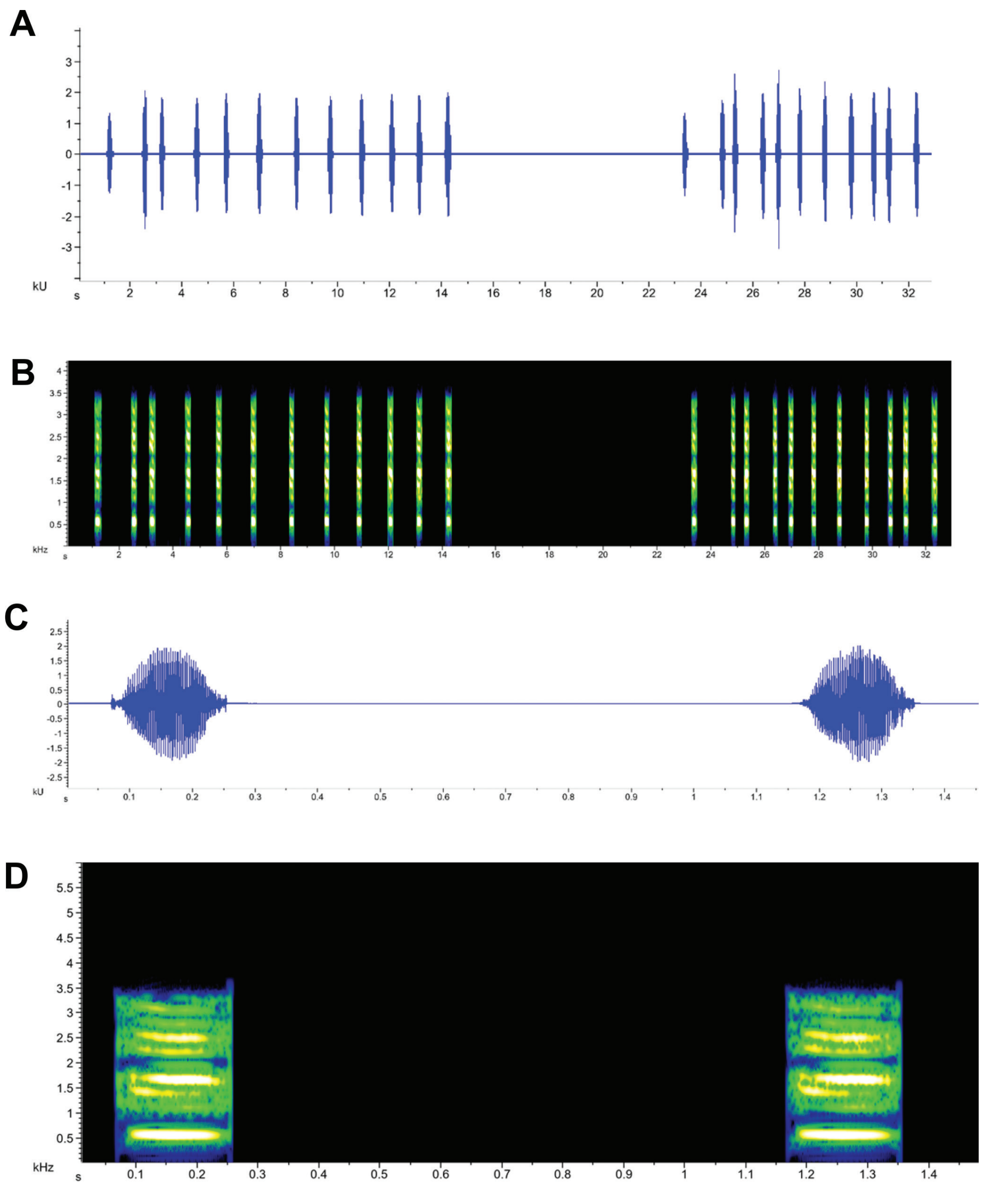

Figure 4. The call of *Kaloula discordia* sp. nov. from Cat Tien NP, Dong Nai Province, Vietnam. **A.** 33 s waveform of relative amplitude (Rel. amp.) and corresponding spectrogram over time; **B.** 1.5 s waveform and corresponding spectrogram of two calls, obtained from the last two calls in (**A**). Data on acoustic characters is summarized in Table 4.

Table 3. Comparison of male advertisement calls for *Kaloula discordia* sp. nov. and other members of the *K. baleata* species complex. NR: not recorded.

Species	*Kaloula discordia* sp. nov.	*Kaloula indochinensis*	*Kaloula baleata*	*Kaloula ghoshi*
Locality	Cat Tien NP, Tan Phu District, Dong Nai Province, Vietnam	Kon Von II village, Dak Roong Commune, K'Bang District, Gia Lai Province, Vietnam	Kinabalu, Sabah, Malaysia	Hut Bay, Little Andaman Island
Coordinates	11.411°N, 107.419°E	14.543°N, 108.414°E	NR	NR
Number of calls measured	23	40	NR	NR
Call duration (ms)	186.1 (144–214)	215.6 (194–250)	280–300	400 (320–640)
Intercall interval (ms)	1539.4 (851–8954)	789.3 (481–1627)	NR	300 (240–530)
Call repetition rate (call/s)	1.0 (0.75–1.21)	1.0 (0.76–1.25)	NR	NR
Call repetition rate (call/minute)	56.5 (42–71)	60.1 (45.9–75.2)	NR	NR
Notes/call	1	1	NR	NR
Pulse/call	11–13	1*	Described as pulsed	7–25
Dominant frequency (kHz)	0.38 (0.30–0.45)	0.38 (0.34–0.43)	1–3	1
2nd harmonic (kHz)	1.0	0.8	NR	NR
3rd harmonic (kHz)	1.2	1.2	NR	NR
4nd harmonic (kHz)	1.5	1.37	NR	NR
Temperature (°C)	24.0	20.5	23.0	29.1
Source	this study	Nguyen et al. (2022)	Malkmus et al. (2002)	Chandramouli and Prasad (2018)

Table 4. Measurements (in mm) of specimens of *Kaloula discordia* sp. nov., *Kaloula laosensis* sp. nov., and *K. indochinensis*. For character abbreviations, see the Materials and methods section. Abbreviations: F – adult female; M – adult male; SF – subadult female; SM – subadult male.

Species	Sample ID	Sex	Status	SVL	HL	SL	EL	N-EL	HW	IND	IOD	UEW	FLL	LAL	HAL	1FL	IPTL	OPTL	3FDD	HLL	TL	FL	OMTL	1TOEL	4TDD
Kaloula discordia **sp. nov.**	ZMMU-A-8134	**M**	holotype	51.5	11.7	5.5	4.1	3.9	14.8	3.2	5.3	3.0	31.9	26.4	15.7	8.1	3.0	3.5	3.6	60.0	14.7	30.2	2.1	7.9	2.3
K. discordia **sp. nov.**	ZMMU-A-4739	**M**	paratype	52.0	11.9	5.2	4.0	3.9	15.2	3.2	5.3	2.9	33.4	26.8	15.8	8.2	3.0	3.4	3.8	62.7	15.3	31.4	2.5	7.7	2.9
K. discordia **sp. nov.**	ZISP 15285	**M**	paratype	48.0	10.8	5.1	3.1	3.7	13.7	3.1	5.0	2.8	31.2	24.1	15.0	7.8	2.9	3.3	3.2	58.0	13.4	28.9	2.5	7.9	2.6
K. discordia **sp. nov.**	ZMMU-A-8135	**M**	paratype	49.6	11.3	5.3	3.4	3.8	14.0	3.2	4.9	2.7	31.5	25.3	15.3	7.9	2.6	3.3	3.5	59.0	14.1	29.7	2.4	7.6	2.8
K. discordia **sp. nov.**	ZMMU-A-8136	**M**	paratype	45.4	10.6	4.9	3.3	3.4	13.8	3.0	4.8	2.7	31.4	24.2	14.6	7.8	2.9	2.8	3.3	57.4	14.1	27.9	2.2	7.2	2.4
K. discordia **sp. nov.**	ZMMU-A-8137	**M**	paratype	42.9	10.3	4.9	3.0	3.0	13.7	3.0	4.5	2.6	30.8	24.0	14.9	7.8	2.3	3.1	3.0	56.3	13.1	28.5	2.0	7.1	2.4
K. discordia **sp. nov.**	ZMMU-A-8138	**M**	paratype	48.7	11.1	5.3	3.7	3.5	14.7	3.2	4.9	2.9	31.1	25.0	15.4	7.9	2.4	3.0	3.5	60.6	14.4	30.5	2.2	7.4	2.3
K. discordia **sp. nov.**	ZMMU-A-8139	**M**	paratype	49.5	11.2	5.1	3.1	3.5	15.0	3.1	4.7	3.0	31.7	24.9	14.2	7.4	2.6	3.1	3.3	60.5	13.8	31.0	1.9	7.5	2.7
K. discordia **sp. nov.**	ZMMU-A-8140	**M**	paratype	47.2	10.5	5.0	3.4	3.3	15.1	3.0	4.9	2.7	27.9	23.0	14.1	6.8	2.7	3.3	3.5	57.6	14.7	27.4	1.9	6.9	2.8
K. discordia **sp. nov.**	ZISP 15286	**M**	paratype	52.6	12.2	5.8	3.8	3.8	15.7	3.2	5.6	2.8	32.9	26.3	15.6	7.9	3.2	3.6	4.0	61.9	15.1	31.1	2.3	8.2	3.4
K. discordia **sp. nov.**	ZISP 15287	**M**	paratype	49.1	10.6	5.3	3.6	3.5	14.5	3.1	5.0	2.7	31.2	24.6	15.4	8.1	2.8	3.1	3.4	60.6	14.3	29.7	2.6	8.2	2.6
K. discordia **sp. nov.**	ZMMU-A-8141	**M**	paratype	50.0	11.3	5.5	3.5	3.7	15.3	3.2	5.0	3.0	31.8	25.2	15.2	7.5	2.6	3.0	3.3	60.5	14.3	31.0	1.9	7.4	2.6
K. discordia **sp. nov.**	ZMMU-A-8142	**M**	paratype	52.2	11.7	5.1	3.6	3.2	15.3	3.2	5.0	2.8	31.9	25.1	15.6	7.9	2.5	3.0	3.6	61.0	14.1	30.8	1.9	7.2	2.7
K. discordia **sp. nov.**	ZMMU-A-8143	**M**	paratype	51.5	11.7	5.5	3.4	3.6	15.0	3.2	5.1	2.7	32.1	25.4	15.2	7.9	2.9	3.1	3.7	58.5	13.4	29.9	2.4	7.5	2.6
K. discordia **sp. nov.**	ZMMU-A-4642	**F**	paratype	56.2	12.8	6.2	4.1	4.2	17.0	3.8	5.9	3.0	35.9	28.2	16.3	9.3	3.2	3.7	4.0	67.4	16.7	33.3	3.0	9.0	3.0
K. discordia **sp. nov.**	ZMMU-A-4602-1	**F**		56.4	13.0	5.4	4.2	4.0	16.9	3.7	6.0	3.0	35.8	28.6	16.6	10.0	3.4	3.4	3.8	67.6	17.2	33.7	3.0	9.1	2.9
K. discordia **sp. nov.**	ZMMU-A-4602-2	**SF**		25.3	7.0	3.1	2.5	2.8	7.5	1.9	3.2	1.5	15.5	11.9	7.0	3.8	2.0	1.8	1.7	30.2	7.4	13.9	-	3.5	1.5
K. discordia **sp. nov.**	ZMMU-A-4602-3	**SF**		35.0	8.3	3.8	3.0	2.8	10.2	2.6	3.6	1.9	23.2	14.5	10.3	5.9	2.2	2.2	2.6	40.2	9.6	20.4	1.4	4.5	2.0
Kaloula laosensis **sp. nov.**	ZISP 15284	**M**	holotype	44.0	10.6	4.6	3.3	3.2	12.6	2.7	4.3	2.4	27.6	21.7	13.0	7.5	2.7	2.8	3.4	49.3	11.6	25.4	2.0	7.3	2.2
K. laosensis **sp. nov.**	ZMMU-A-8144	**F**	paratype	54.8	12.4	5.3	5.0	5.2	16.5	3.6	5.7	3.0	33.8	28.3	17.8	10.4	3.2	3.7	4.3	66.9	16.4	32.5	2.8	8.4	2.8
Kaloula indochinensis	ZMMU-A-8147	**M**		45.3	11.0	4.9	3.9	3.3	14.7	3.1	5.0	2.8	31.5	23.7	13.9	8.1	3.1	3.4	3.8	55.2	14.0	27.2	2.19	7.2	2.3
K. indochinensis	ZMMU-A-8148	**M**		50.9	11.6	5.3	3.4	3.8	15.1	3.0	4.5	2.5	32.5	24.8	14.6	7.9	2.9	3.1	3.3	57.3	14.5	27.5	2.72	8.1	2.4
K. indochinensis	ZMMU-A-8149	**M**		42.3	9.8	4.8	3.4	3.3	12.0	2.9	4.5	2.4	28.1	20.4	12.6	7.8	2.4	2.6	2.9	47.9	10.9	24.9	2.15	6.2	2.2
K. indochinensis	ZMMU-A-8150	**M**		46.3	10.7	4.9	3.5	3.5	13.0	3.1	4.5	2.6	29.9	22.4	13.9	7.9	2.6	3.0	3.4	50.7	12.2	26.2	2.59	7.0	2.4
K. indochinensis	ZMMU-A-8151	**M**		48.5	11.2	5.2	3.9	3.5	15.7	3.1	4.7	2.7	31.1	24.0	14.6	8.2	3.2	3.3	3.7	55.1	12.9	27.6	2.44	7.4	2.7
K. indochinensis	ZMMU-A-8152	**M**		49.1	11.9	5.3	4.0	3.8	15.0	3.3	5.1	2.8	30.6	24.4	14.9	8.7	3.1	3.2	3.6	55.9	12.7	27.5	2.35	7.4	2.3
K. indochinensis	ZMMU-A-8153	**M**		48.8	11.8	4.9	4.0	3.6	15.3	3.0	5.0	2.7	31.3	24.3	14.5	7.8	2.9	3.3	3.6	53.0	12.7	26.2	2.80	6.6	2.5
K. indochinensis	ZMMU-A-8154	**M**		49.8	11.9	5.5	3.9	3.5	16.3	3.4	5.0	2.7	32.0	24.3	15.1	8.4	2.7	3.1	3.8	54.5	12.9	27.5	2.62	7.4	2.5
K. indochinensis	ZMMU-A-6316	**M**	topotype	50.4	11.7	5.2	4.0	3.7	14.9	3.2	4.9	2.9	28.1	22.8	14.5	8.6	3.2	3.3	3.1	54.7	12.4	27.0	2.75	6.8	2.3
K. indochinensis	ZMMU-A-6317	**M**	topotype	47.3	10.8	5.1	3.8	3.3	14.1	3.0	4.9	2.9	26.7	22.0	13.9	8.0	2.7	2.9	2.8	52.2	12.2	25.7	2.89	5.9	1.8
K. indochinensis	ZMMU-A-6318	**M**	topotype	51.1	11.6	5.4	3.9	3.5	16.2	3.3	5.2	2.7	31.7	25.2	15.5	8.9	3.4	3.4	3.5	55.8	13.0	27.5	2.84	7.1	2.2
K. indochinensis	ZMMU-A-6319	**M**	topotype	59.6	12.7	5.8	4.1	4.0	17.7	3.4	5.8	3.1	34.3	28.6	18.1	10.4	3.9	4.4	4.2	63.9	15.0	31.6	2.79	8.5	2.8
K. indochinensis	ZMMU-A-6320	**M**	topotype	51.3	12.3	5.3	4.0	3.8	15.9	3.4	5.3	2.9	30.5	24.9	15.7	9.2	3.3	3.2	3.4	55.4	13.1	27.3	2.79	7.7	2.2
K. indochinensis	ZMMU-A-6321	**M**	topotype	50.0	12.3	5.3	4.0	3.7	16.1	3.4	5.4	3.2	28.4	24.0	14.7	8.8	2.9	3.4	3.4	55.7	13.4	27.5	3.22	7.0	2.1
K. indochinensis	ZMMU-A-6322	**M**	topotype	50.5	12.4	6.0	4.2	4.2	16.5	3.6	5.7	3.0	30.4	24.9	15.7	9.4	3.5	3.5	3.9	57.8	13.9	28.8	2.88	7.8	2.4
K. indochinensis	ZMMU-A-6323	**M**	topotype	51.7	11.4	5.4	4.0	3.7	15.0	3.6	5.9	3.3	31.3	25.3	15.8	9.2	3.6	3.9	3.2	58.0	14.1	28.0	2.85	7.4	2.4
K. indochinensis	ZMMU-A-6324	**M**	topotype	50.2	12.4	5.5	4.0	3.5	15.7	2.9	5.0	3.1	29.1	23.6	14.6	8.2	3.3	3.4	3.2	55.7	13.6	26.5	2.97	7.0	2.2
K. indochinensis	ZMMU-A-6325	**M**	topotype	48.2	10.7	5.1	3.9	3.7	14.3	3.3	5.1	3.0	28.8	23.1	14.4	7.8	2.7	2.9	3.4	53.9	12.4	26.3	2.65	6.7	2.1
K. indochinensis	ZMMU-A-6315	**F**	topotype	55.2	13.1	6.2	4.3	4.4	17.3	3.4	5.8	3.1	32.9	27.9	18.0	9.8	3.2	3.8	4.0	62.7	14.8	31.9	3.08	8.4	2.5
K. indochinensis	ZMMU-A-8155	**SF**		36.1	8.7	4.4	3.4	2.9	11.6	2.6	3.9	2.1	24.8	18.8	11.7	5.9	2.2	2.4	3.0	41.6	10.4	21.3	1.69	5.7	2.1

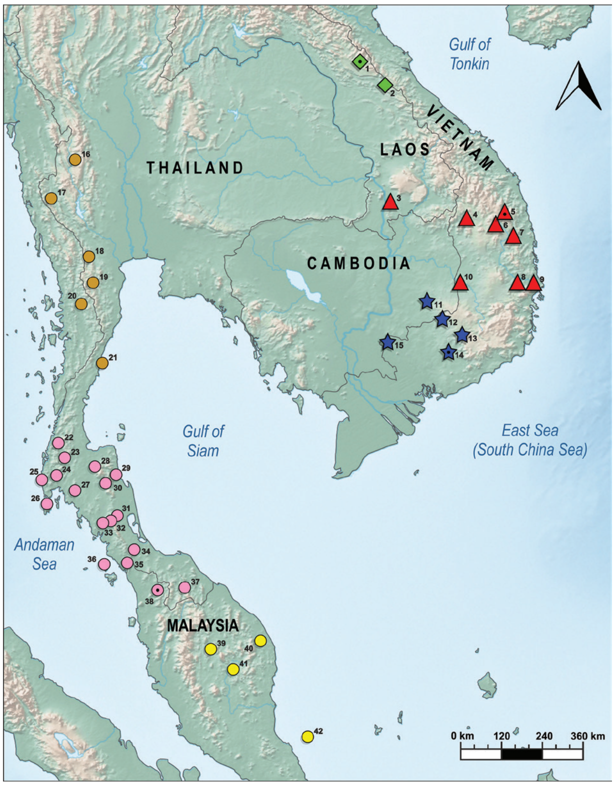

Figure 5. Known distribution of the *Kaloula baleata* species complex members in Indochina. Dots within symbols denote type localities. Symbol colors correspond to mitochondrial DNA lineages (Figs 1, 2. Note that the tentative assignment of the populations that were not sequenced is based on geographic proximity and/or examination of morphological or photographic data from these populations). Symbol numbers correspond to locality numbers given in Appendix 1.

Description of the holotype (Fig. 6). Adult male in a good state of preservation, habitus robust, head wider than long (HW/HL 1.27), snout projecting beyond lower jaw, gently rounded in lateral view (Fig. 6C); truncated in dorsal view; top of head flat; upper eyelid lacking supraciliary tubercles; eye length less than snout length (EL/SL 0.74) and less than interorbital distance (EL/IOD 0.76); pupils round; nostrils rounded, placed more towards the lateral sides of the snout, located closer to tip of snout than to eye, relatively close to each other (IND/IOD 0.60); supratympanic fold flat, glandular, rather thin; tympanum not visible (Fig. 6C); dorsal surfaces of body and limbs with sparse tubercules, getting denser backwards; ventral surfaces of body and limbs with flat tubercules (Fig. 6A, B). Cloacal opening unmodified, directed posteriorly. Forelimbs relatively long, more than a half of hind limb length (FLL/HLL 0.53); hand long, comprising more than a half of lower arm length (HAL/LAL 0.60) and almost half of forelimb length (HAL/FLL 0.49); fingers rather robust, notably flattened in cross section; relative finger lengths: I<II<IV<III; fingers free of webbing; terminal digits flattened forming wide transversely expanded disks (Fig. 6E); finger subarticular tubercles distinct, large and round, finger subarticular tubercle formula 1:1:2:2; inner metacarpal tubercle elongate; outer metacarpal tubercule triangular-shaped, dilated, bigger than inner metacarpal tubercle (OPTL/IPTL1.18), two metacarpal tubercles not in touch with each other (Figs 6E, 9C); hindlimbs robust, relatively short, not much longer than body length (HLL/SVL 1.16); relative toe lengths: I<II<V<III<IV; tarsal fold on inner surface of tarsus absent; tips of all toes widened, forming rounded terminal disks; all toe disks having dorso-terminal groves; the disk on toe IV the largest (Figs 6D, 9C); toe webbing well developed between all toes, reaching disks at all toes except toe IV; webbing formula I1-2II1.5-2.5III1.5-3IV3-1.5V; toe subarticular tubercules distinct, rounded; toe subarticular formula 1:1:2:2:2; two metatarsal tubercles, inner metatarsal tubercle elongated, oval; outer metatarsal tubercle smaller, rounded (Figs 6D, 9C).

Coloration. In life, the dorsal surfaces of the head and body olive-brown, dorsal surfaces of the limbs grayish-olive with grayish-white spots (Fig. 6A); flanks of the body and lateral sides of the head grayish olive; orange-brown 8-shaped patches on the neck posterior to eyes; bright-orange axillary patch continuing on elbows (Fig. 7C); grayish-white inguinal patch; small grayish-beige spots near tibiotarsal articulation; ventral surfaces of head and body gray, darker on the throat near the jaw; belly and ventral surfaces of limbs pinkish with weak white mottling (Fig. 6B). Iris golden with brown reticulations ventrally and dorsally from the pupil (Figs 6C, 7C). In preservation after one year of storage in ethanol, dorsal coloration faded to dark gray, light patches became less pronounced, and they faded to light gray or grayish-beige, though the pattern generally remained unchanged.

Measurements of the holotype (in mm): SVL 51.5; HL 11.7; HW 14.8; SL 5.5; EL 4.1; N-EL 3.9; IND 3.2; IOD 5.3; UEW 3.0; FLL 31.9; LAL 26.4; HAL 15.7; HLL 60.0; TL 45.0; FL 30.2; IPTL 3.0; OPTL 3.5; 1FL 8.1; 1TOEL 7.9; OMTL 2.1; 3FDD 3.6; 4TDD 2.3.

Variation. Table 4 presents the morphometric variation of the type series. Fig. 8 displays the variation in dorsal coloration of the paratypes. In general, all paratypes agree well with the description of the holotype, differing only in the brightness of light inguinal and axillary markings. In male paratypes ZISP 15285 and ZMMU A-8138, the right foot is poorly developed; in male paratype ZMMU A-8139, the right hand is poorly developed.

Tadpole morphology. Vassilieva (2021) provided morphometric data and a detailed description of tadpoles of *Kaloula discordia* sp. nov. (as *K. indochinensis*). Vassilieva (2021) noted that tadpoles of '*K. indochinensis*' from Cat Tien NP, Dong Nai Province, southern Vietnam (corresponding to *Kaloula discordia* sp. nov.) differ from *K. indochinensis* sensu stricto from Kon Ka Kinh NP, Gia Lai Province, and Chu Mon Ray NP, Kon Tum Province, central Vietnam, by having comparatively longer spiracle tubes (markedly longer than the vent tubes), a narrower mouth relative to body width, more developed tail musculature (tail base width more than a third of the body width), and a rather contrasting tail coloration.

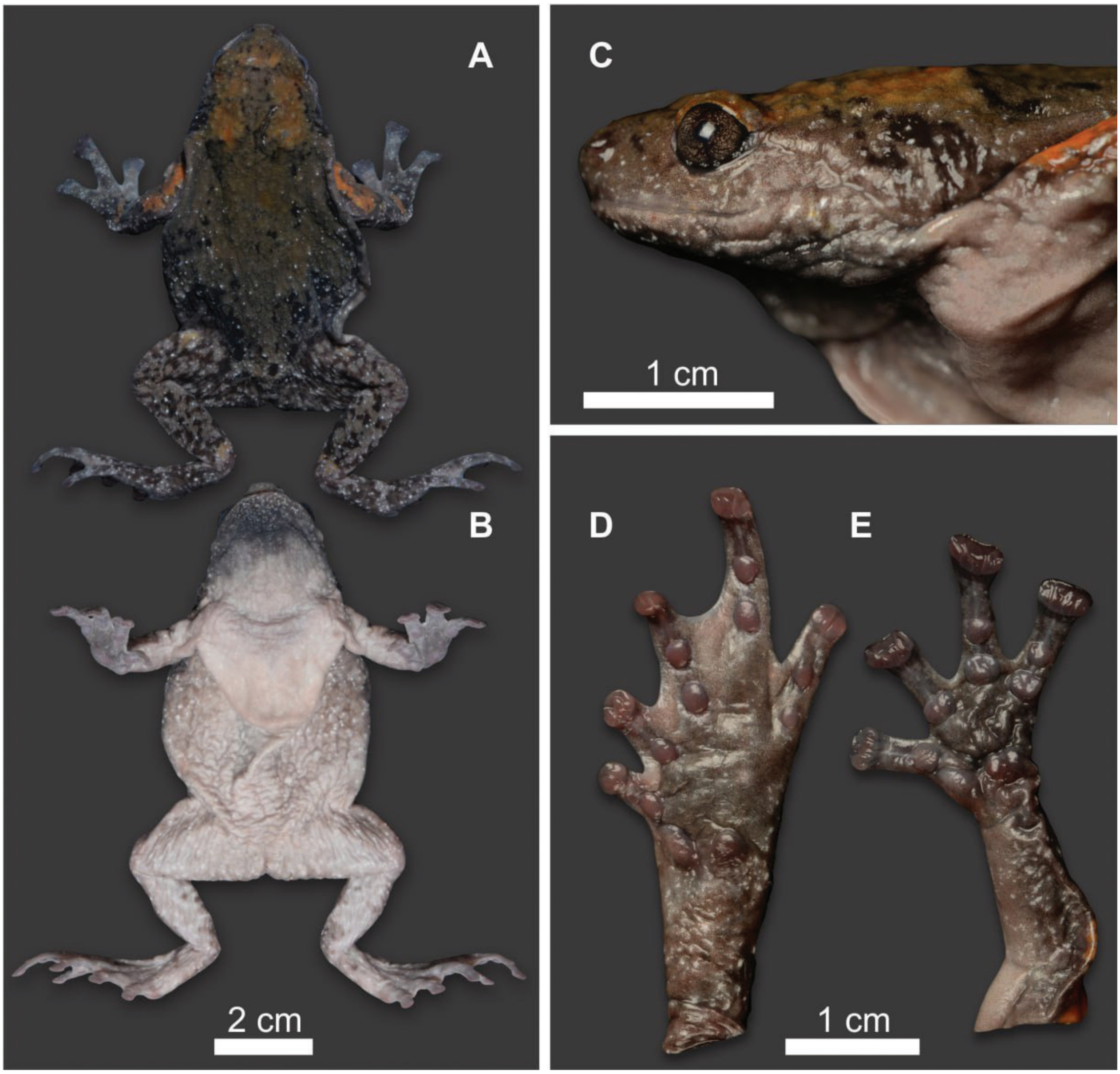

Figure 6. Holotype of *Kaloula discordia* sp. nov. (ZMMU A-8134), adult male. **A.** Dorsal view; **B.** Ventral view; **C.** Head in a lateral view; **D.** Plantar view of left foot; **E.** Volar view of left hand. Photographs by N.A. Poyarkov.

Distribution and natural history. *Kaloula discordia* sp. nov. is currently reliably known from Dong Nai, Lam Dong, Tay Ninh, and Binh Phuoc provinces of Southern Vietnam and was also reported from the adjacent Mondulkiri Province of eastern Cambodia; the known distribution of the new species is shown in Fig. 5, and the locality information is detailed in Appendix 1. The single Cambodian record of the new species from Phnom Prich Wildlife Sanctuary in Mondulkiri Province, originally reported as *K. indochinensis* by Chan et al. (2013) and Holden (2023), can be confidently assigned to *Kaloula discordia* sp. nov. based on the external morphology and coloration of the recorded specimen and the geographic proximity of the locality to the population of *Kaloula discordia* sp. nov. in Binh Phuoc Province of southern Vietnam. The new species was recorded mostly from relatively low elevations of ca. 70–300 m a.s.l.; in Bao Loc forestry of Lam Dong Province, the new species was recorded at elevations up to 550 m a.s.l. *Kaloula discordia* sp. nov. is restricted to lowland and hilly, seasonally dry, semi-deciduous, and evergreen monsoon forests of southern Vietnam (see Vassilieva et al. 2016). Male frogs were recorded calling from small temporary pools and flooded areas from May to November (Fig. 7A, B); the peak of the breeding season coincides with heavy rains in June–August. The new species is semi-fossorial and quite elusive and is usually active only after periods of heavy rains; frogs are aestivating during dry periods in leaf litter, underground borrows, or tree hollows (Vassilieva et al. 2016; Holden 2023). Diet consists of ants and beetles (Vassilieva et al. 2016); the new species is a good climber; males can call when perching a few meters above ground level (Holden 2023). The actual distribution of *K. discordia* sp. nov. is still insufficiently known, but we suppose that this species

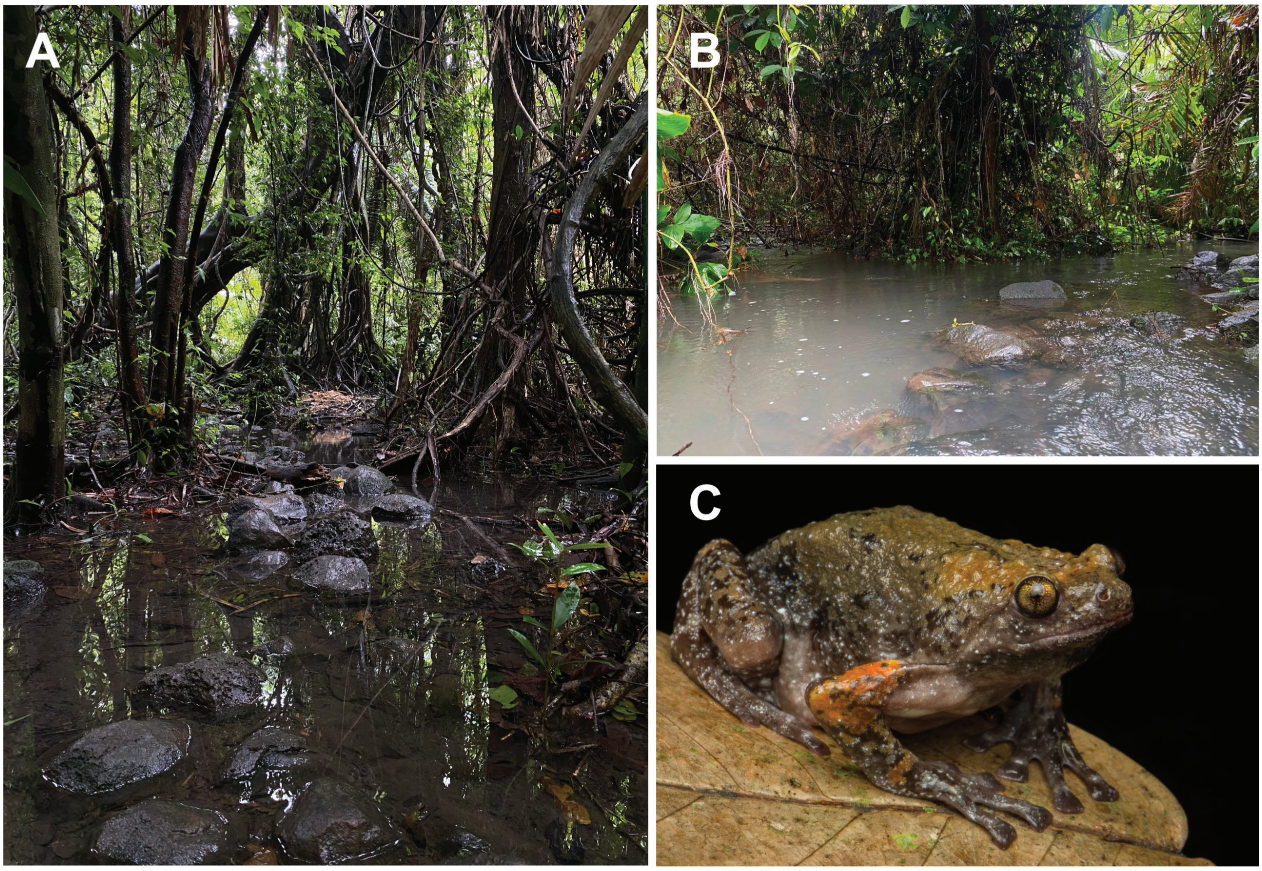

Figure 7. Breeding habitats of *Kaloula discordia* sp. nov. (**A, B**) and lateral view of holotype of *Kaloula discordia* sp. nov. in situ (ZMMU A-8134) (**C**). Photographs by A.M. Bragin.

is likely to occur in those provinces of southern Vietnam where forests similar in composition are still preserved, including Dak Nong, Binh Duong, Binh Thuan, and Ba Ria-Vung Tau provinces. Syntopic species of amphibians included *Microhyla butleri* Boulenger, 1900; *M. heymonsi* Vogt, 1911; *M. mukhlesuri*; *Kaloula pulchra*; *Fejervarya limnocharis* (Gravenhorst, 1829); *Occidozyga martensii*; *Polypedates megacephalus* Hallowell, 1861; and *Rhacophorus annamensis* Smith, 1924.

Comparisons. *Kaloula discordia* sp. nov. most closely resembles other frogs of the *K. baleata* species complex in overall morphology; most specifically, it is similar to *K. indochinensis*, with which it was previously confused. From *K. indochinensis*, the new species can be distinguished by having generally smaller eye size in males (EL mean 3.5 ± 0.3 mm [n = 14] vs. mean 3.9 ± 0.2 mm [n = 18]; EL/SVL 0.071 ± 0.004 vs. 0.079 ± 0.004); smaller finger I in males (1FL mean 7.8 ± 0.4 mm [n = 14] vs. mean 8.5 ± 0.7 mm [n = 18]; 1FL/SVL 0.16 ± 0.01 vs. 0.17 ± 0.007); generally smaller inner palmar tubercules in males (IPTL mean 2.8 ± 0.3 mm [n = 14] vs. mean 3.1 ± 0.4 mm [n = 18]; IPTL/SVL 0.056 ± 0.004 vs. 0.062 ± 0.005); and generally smaller outer palmar tubercules in males (OPTL mean 3.2 ± 0.2 mm [n = 14] mm vs. mean 3.3 ± 0.4 mm [n = 18]; OPTL/SVL 0.064 ± 0.004 vs. 0.067 ± 0.005); generally longer hindlimbs in both sexes (HLL mean 59.6 ± 1.9 mm [n = 14] in males, mean 67.5 ± 0.2 mm [n = 2] in females vs. mean 55.2 ± 3.3 mm [n = 18] in males; 62.7 mm [n = 1] in female; HLL/SVL 1.21 ± 0.04 vs. 1.12 ± 0.03 in both sexes); smaller metatarsal tubercule in males (OMTL mean 2.2 ± 0.3 mm [n = 14] vs. mean 2.7 ± 0.3 mm [n = 18]); by having two metacarpal tubercles, see Fig. 9C (vs. three metacarpal tubercles, see Fig. 9B); by having two subarticular tubercles on toe IV, see Fig. 9C (vs. three well-developed subarticular tubercles, see Fig. 9B); and by having olive dorsal coloration (vs. chocolate-brown to dark grayish-brown).

From *K. baleata* (morphological data taken from Chan et al. 2013), *Kaloula discordia* sp. nov. can be distinguished by having generally smaller eyes in both sexes (EL mean 3.5 ± 0.3 mm [n = 14] in males, mean 4.2 ± 0.01 mm [n = 2] in females vs. mean 4.1 ± 0.4 mm [n = 10] in males, mean 4.5 ± 1.7 mm [n = 2] in females); larger distance between nares in both sexes (IND mean 3.1 ± 0.1 mm [n = 14] in males, mean 3.7 ± 0.1 mm [n = 2] in females vs. mean 2.7 ± 0.4 mm [n = 10] in males, mean 3.1 ± 0.30 mm [n = 2] in females); wider finger III disks in both sexes (3FDD mean 3.5 ± 0.3 mm [n = 14] in males, mean 3.9 ± 0.1 mm [n = 2] in females vs. mean 1.7 ± 0.2 mm [n = 10] in males, mean 2.1 ± 0.6 mm [n = 2] in females); smaller metatarsal tubercule in males (OMTL mean 2.2 ± 0.3 mm [n = 14] vs. mean 3.2 ± 0.2 mm [n = 10]); and by having two subarticular tubercles on toe IV, see Fig. 9C (vs. three well-developed subarticular tubercles).

Figure 8. Variation in dorsal coloration in paratypes of *Kaloula discordia* sp. nov. Scale bar equals 5 cm. Photographs by N.A. Poyarkov.

From *K. latidisca* (morphological data taken from Chan et al. 2014), the new species can be distinguished by having shorter head in males (HL mean 11.2 ± 0.6 mm [n = 14] vs. mean 14.4 ± 0.8 mm [n = 4]); narrower head in males (HW mean 14.7 ± 0.7 mm (n = 14) vs. mean 18.7 ± 1.1 mm [n = 4]); smaller distance between nares in males (IND mean 3.1 ± 0.1 mm [n = 14] vs. mean 4.0 ± 0.1 mm [n = 4]); smaller distance between eyes in males (IOD mean 5.0 ± 0.2 mm [n = 14] vs. mean 5.7 ± 0.4 mm [n = 4]); smaller eye in males (EL mean 3.5 ± 0.3 mm [n = 14] vs. mean 4.6 ± 0.3 mm [n = 4]); smaller metatarsal tubercle in males (OMTL mean 2.2 ± 0.3 mm [=14] vs. mean 3.4 ± 0.1 mm [n = 4]); and by having two subarticular tubercles on toe IV, see Fig. 9C (vs. three subarticular tubercles).

Furthermore, *Kaloula discordia* sp. nov. differs from *K. aureata* Nutphand, 1989, by having an olive dorsum with no dark reticulations (vs. golden dorsum with dark brown reticulations); from *K. borealis* by having wider finger disks (vs. finger tips slightly dilated but not forming wide disks); by yellowish blotches on flanks absent (vs. present); and by olive dorsal coloration (vs. gray-brown). The new species is further diagnosed from *K. conjuncta* by the stratified coloration on flanks absent (vs. present) and by having distinct outer metatarsal tubercle (vs. weak or indistinct). *Kaloula discordia* sp. nov. differs from *K. ghoshi* by having axillary and inguinal light spots (vs. absent); tubercles on dorsum and venter (vs. smooth skin or with small granules dorsally); and olive dorsal coloration (vs. orange-brown). The new species further differs from *K. kalingensis* by having tubercles on the dorsum (vs. dorsum smooth); by having a distinct outer metatarsal tubercle (vs. indistinct); yellow or orange axillary and inguinal spots (vs. usually absent or small and red if present); lacking light pericloacal ring (vs. present); from *K. kokacii* by tuberculated dorsum (vs. smooth); axillary and inguinal spots (vs. absent); from *K. mediolineata* by lacking dorsolateral stripes (vs. present); sacral medial stripe absent (vs. present); and finger disks widened (vs. finger disks slightly

dilated but not forming wide disks). *Kaloula discordia* sp. nov. is distinguished from *K. nonggangensis* by lacking protuberant tubercles on the upper surface of finger tips (vs. present); from *K. picta* by lacking dorsolateral stripes (vs. present); by the stratified coloration on flanks absent (vs. present); and by having wide finger disks (vs. finger disks slightly dilated but not forming wide disks). The new species further differs from *K. pulchra* by the absence of dorsolateral stripes (vs. always present); by having axillary and inguinal spots (vs. absent); from *K. rigida* by having wide finger disks (vs. finger disks slightly dilated but not forming wide disks); by the stratified coloration on flanks absent (vs. present); by the absence of dorsolateral stripes (vs. present); and by having axillary and inguinal spots (vs. absent). *Kaloula discordia* sp. nov. differs from *K. rugifera* by having wide finger disks (vs. slightly expanded small finger disks); by having axillary and inguinal spots (vs. absent); from *K. verrucosa* by having wide finger disks (vs. slightly expanded small finger disks); by having axillary and inguinal spots (vs. absent); from *K. walteri* by having wide finger disks (vs. slightly expanded small finger disks); by the stratified coloration on flanks absent (vs. present); having axillary and inguinal spots (vs. absent); and by having a distinct outer metatarsal tubercle (vs. indistinct or absent). *Kaloula discordia* sp. nov. is geographically isolated from other members of the *K. baleata* species complex and most of the other congeners, except *K. pulchra*, with which it occurs in sympatry everywhere throughout its range, and, possibly, *K. mediolineata*, with which the new species might co-occur in the Tay Ninh, Binh Phuoc, and Ba Ria-Vung Tau provinces of southern Vietnam.

Acoustic data. For a comparison of the male advertisement calls of *Kaloula discordia* sp. nov. with *K. indochinensis* sensu stricto, see Table 3; data for *K. indochinensis* are taken from Nguyen et al. (2022). The power call parameters of *Kaloula discordia* sp. nov. and *K. indochinensis* are quite similar, with the dominant frequency of the call being the same in the two species (0.38 kHz, range 0.34–0.43 kHz vs. 0.38 kHz, range 0.30–0.45 kHz, respectively) (Table 3). At the same time, *Kaloula discordia* sp. nov. had a slightly shorter call duration (186.1 ms, range 144–214 ms) than *K. indochinensis* (215.6 ms, range 194–250 ms) and a significantly longer intercall interval: 1539.4 ms (range 851–8954 ms) in *Kaloula discordia* sp. nov. vs. 789.3 ms (range 481–1627 ms) in *K. indochinensis*. These differences have to be taken cautiously as the records of calling of the two species were taken with different ambient temperatures (20.5 °C for *K. indochinensis* and 24.0 °C for the new species), which also could contribute to the observed differences in call parameters between the two species. Nguyen et al. (2022) did not calculate the number of pulses per call in *K. indochinensis* and noted the presence of one pulse per call in this species (Nguyen et al. 2022: Table 2), while we recorded 11–13 pulses per call in *Kaloula discordia* sp. nov. These differences actually result from the different terminology used by Nguyen et al. (2022) and our study, as the waveform oscillograms in Nguyen et al. (2022) clearly show the presence of several pulses in each call.

Etymology. The specific epithet "*discordia*" is a noun in apposition, in the nominative case, given in reference to the Roman mythological goddess Discordia. According to the poet Hesiod, this goddess personified not only strife and discord but also competition and labor (Hesiod, Theogony: 20–24, 226–230; see Most 2006). The duality of this name echoes the two aspects of the discovery of the new species. The first aspect is the authors' hard work and laborious approach in collecting data for the description of the new species. The second challenge pertains to the authors' internal struggle to choose a politically correct and neutral name for the new species. In modern taxonomy, international teams often face the common challenge of strife and competition; however, this can also lead to overall scientific progress. We recommend "*South Vietnamese Painted Frog*" as the common name in English, "*Yuzhnovietnamskiy Bychiy Uzkorot*" as the common name in Russian, and "*Ễnh ương Nam bộ*" as the common name in the Vietnamese language.

Conservation status. At present, the new species is reliably known only from four localities in southern Vietnam and a single locality in eastern Cambodia (Fig. 5; Appendix 1). The main threats to this species in Vietnam are habitat loss and degradation. The new species is restricted to the lowland monsoon tropical forests of southern Vietnam; it should be noted that these forests during the last 40 years have been subjected to greater anthropomorphic conversion (including logging, agriculture, road construction, and other human activities) than other areas in Vietnam (e.g., De Koninck 1999; Kuznetsov and Kuznetsova 2011; Laurance 2007; Meijer 1973; Meyfroidt and Lambin 2008). The range of the new species covers several nature conservation areas of southern Vietnam and Cambodia, including Cat Tien NP (Dong Nai Biosphere Reserve), Bu Gia Map NP, Lo Go-Xa Mat NP (Vietnam), and Phnom Prich Wildlife Sanctuary (Cambodia). Given the lack of comprehensive studies on the adjacent territories, we suggest *Kaloula discordia* sp. nov. be classified as Data Deficient (DD) according to the IUCN's Red List categories (IUCN 2019).

Kaloula laosensis Poyarkov, Orlov, Gorin & Milto, sp. nov.

https://zoobank.org/BF91FDDB-DE05-4518-96E5-E9151DDDF87F

Figs 2, 9A, 10–12, Table 4

Chresonymy. *Kaloula baleata* [partim]—Orlov and Ananjeva (2007: 148); Nguyen et al. (2009: 94).

Kaloula indochinensis [partim]—Chan et al. (2013: 334, 2014: 577); Teynié et al. (2014: 29); Chandramouli and Prasad (2018: 52); Poyarkov et al. (2021b: 39); Holden (2023: 148).

Holotype. ZISP 15284 (field label ZISP 199), adult male, Na Home Village, Bouphala District, near the border of Nakai-Nam Theun National Park, Khammouane Province, Laos, collected by N.L. Orlov, S.N. Nguyen, and K.D. Milto on June 18, 2009 (17.544528°N, 105.695278°E; elevation 174 m a.s.l.).

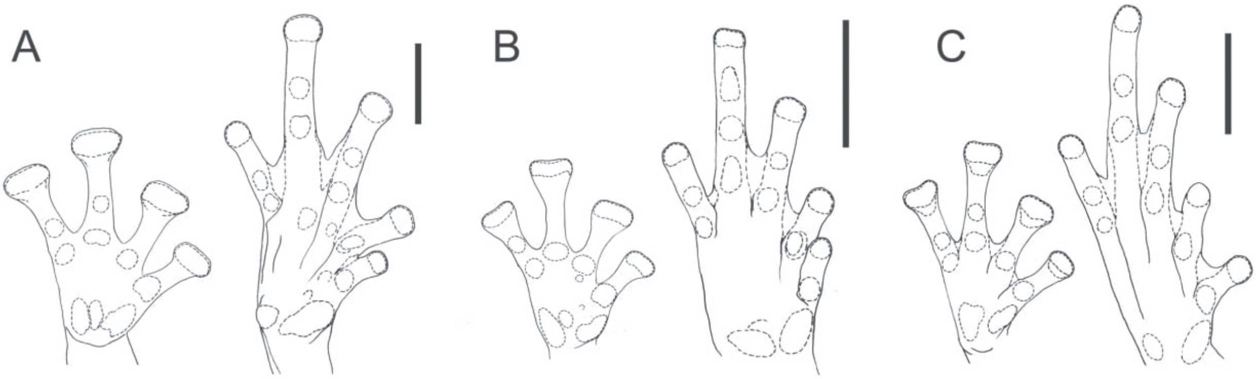

Figure 9. Morphological details of feet and hands in the three species of the *Kaloula baleata* species complex of eastern Indochina. **A.** Volar view of the left hand and plantar view of the right foot of *Kaloula laosensis* sp. nov.; **B.** Volar view of the left hand and plantar view of the right foot of *K. indochinensis*; **C.** Volar view of the left hand and plantar view of the right foot of *Kaloula discordia* sp. nov. Scale bar equals 5 mm. Drawings by N.A. Poyarkov.

Paratype (n = 1). ZMMU A-8144 (field label ZISP 200), adult female from the same location and with the same collection data as the holotype.

Diagnosis. *Kaloula laosensis* sp. nov. is distinguished from its congeners by the following combination of morphological attributes: (1) medium size (SVL ranging 44.0–54.8 mm); (2) eyes comparatively large (eye length comprising 75%–100% of snout length); (3) dark-brown dorsally, with numerous irregular dark blotches forming pericloacal ring; (4) gray or beige ventrally with dense white mottling on belly and limbs; (5) orange triangular patch on either side of the neck posterior to eyes; (6) bright-orange axillary patch present; (7) orange inguinal patch present; (8) bright-orange butterfly-shaped blotch above cloaca present; (9) gray spot on tibiotarsal articulation present; (10) dark interorbital bar present; (11) enlarged, widened finger disks (7.8%–7.9% of SVL), ca. 1.53 times wider than toe disks; (12) finger subarticular tubercle formula: 1:1:2:2; (13) toe subarticular tubercle formula: 1:1:2:2:2; (14) three metacarpal tubercles, median metacarpal tubercle in contact with inner metacarpal tubercle; (15) two metatarsal tubercles, inner metatarsal tubercle ca. three times larger than outer metatarsal tubercle; (16) three small supernumerary tubercles at the basis of toes I, III, IV.

Description of the holotype (Fig. 10). Adult male in a good state of preservation, habitus robust; head wider than long (HW/HL 1.19); snout projecting beyond lower jaw, truncated in dorsal and lateral views (Fig. 10C); top of head flat; upper eyelid lacking supraciliary tubercles; eye length less than snout length (EL/SL 0.75) and less than interorbital distance (EL/IOD 0.77); pupils round; nostrils rounded, placed more towards the lateral sides of snout, located closer to tip of snout than to eye, relatively close to each other (IND/IOD 0.63); supratympanic fold flat, tubercular; tympanum not visible (Fig. 10C); dorsal surfaces of body and limbs with sparse tubercules, getting denser backwards; ventral surfaces of body and limbs almost smooth (Fig. 10A, B). Cloacal opening unmodified, directed posteriorly. Forelimbs relatively long, more than a half of hind limb length (FLL/HLL 0.63); hand long, comprising more than a half of lower arm length (HAL/LAL 0.6) and almost half of forelimb length (HAL/FLL 0.47); fingers rather robust, flattened in cross section; relative finger lengths: I<II<IV<III; no webbing between fingers; terminal digits flattened into very wide transversely expanded T-shaped disks (Fig. 10E); finger subarticular tubercles distinct, protuberant, large and round, finger subarticular formula: 1:1:2:2; metacarpal tubercles three (Figs 9A, 10E), inner metacarpal tubercle elongate, flattened; outer metacarpal tubercule oval, dilated, slightly bigger than inner (OPTL/IPTL 1.05), median metacarpal tubercle the smallest, oval-shaped, contacting both the inner and outer metacarpal tubercles (Figs 9A, 10E); hindlimbs robust, relatively short, not much longer than body length (HLL/SVL 1.12); relative toe lengths: I<II<V<III<IV; tarsal fold on inner surface of tarsus absent; tips of all toes widened, forming terminal oval-shaped disks (Figs 9A, 10D); all toe disks having dorso-terminal groves; the disk on toe IV the largest; toe webbing well developed between all toes, reaching disks at all toes except toe IV; webbing formula i1.5-2ii1.5-2.5iii1.5-3iv3-2v; toe subarticular tubercules distinct, rounded, protruding; toe subarticular formula: 1:1:2:2:2; two metatarsal tubercles, inner metatarsal tubercle elongated, oval, shovel-shaped; outer metatarsal tubercle smaller, rounded; three small supernumerary tubercles at the basis of toes I, III, IV (Figs 9A, 10D).

Coloration. In life, dorsal surfaces of head and body dark brown with contrasting black spots and blotches; black interorbital bar between the upper eyelids; irregular black blotch on the snout; a series of black blotches forming a L-shaped chevron pattern in the scapular region; elongated black blotches on mid-dorsum, body flanks, and sacral area, forming a black pericloacal ring with irregular borders (Figs 2, 11); dorsal surfaces of limbs grayish brown with dark-brown to black blotches; flanks of body and lateral sides of head grayish brown; on lateral sides of belly getting dark-brown with white spots and blotches; pale orange patches on the neck posterior to eyes; bright reddish-orange axillary patch edged with dark brown; bright reddish-orange inguinal patch edged

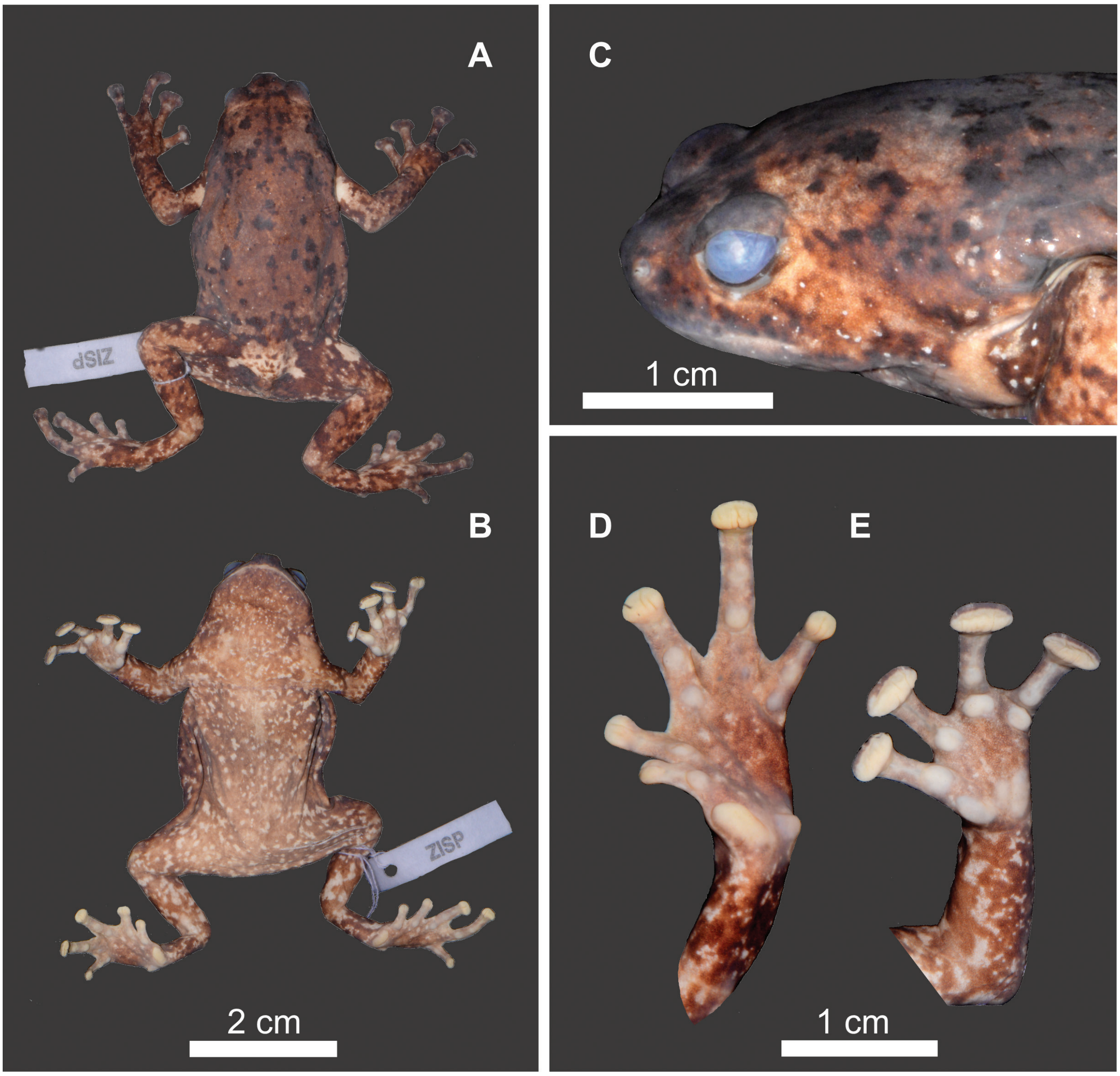

Figure 10. Holotype of *Kaloula laosensis* sp. nov. (ZISP 15284), adult male. **A.** Dorsal view; **B.** Ventral view; **C.** Head in a lateral view; **D.** Plantar view of left foot; **E.** Volar view of left hand. Photographs by V.A. Gorin.

with black; bright reddish-orange patch above cloaca in the center of dark pericloacal ring (Fig. 2); small grayish-beige spots near tibiotarsal articulation; ventral surfaces of head and body gray, darker near the jaw; belly and ventral sides of limbs densely mottled with white spots and dots (Fig. 10); iris chocolate brown with copper sparkles dorsally and ventrally (Fig. 11). In preservation after 15 years of storage in ethanol, dorsal coloration faded to dark grayish-brown; dark markings on dorsum are well descernible; light patches became less pronounced and faded to yellowish or beige in color, though the coloration pattern generally remained unchanged (Fig. 10).

Measurements of the holotype (in mm): SVL 44.0; HL 10.6; HW 12.6; SL 4.6; EL 3.3; N-EL 3.2; IND 2.7; IOD 4.3; UEW 2.4; FLL 27.6; LAL 21.7; HAL 13.0; HLL 49.3; TL 37.0; FL 25.4; IPTL 2.7; OPTL 2.8; 1FL 7.5; 1TOEL 7.3; OMTL 2.0; 3FDD 3.4; 4TDD 2.2.

Variation. Morphometric variation of the type series is presented in Table 4. A dorsal view of a female paratype specimen is presented in Fig. 12. In general, the female paratype specimen agrees well with the description of the holotype, diverging only in body size, which is larger than in the holotype (SVL 54.8 mm). Female paratype ZMMU-A-8144 has comparatively fewer dark markings on the dorsum (Fig. 12), but generally, the coloration pattern is similar to that of the holotype. Holden (2023: 148, fig. 152) published a photo of the new species from Laos as '*K. indochinensis*,' which has bright-red axillary, inguinal, and pericloacal patches and lighter grayish-brown dorsal coloration.

Tadpole morphology. Currently, data on the larval morphology of *Kaloula laosensis* sp. nov. are lacking.

Distribution and natural history. *Kaloula laosensis* sp. nov. is currently reliably known only from two localities in the Khammouane Province of Laos; the distribution

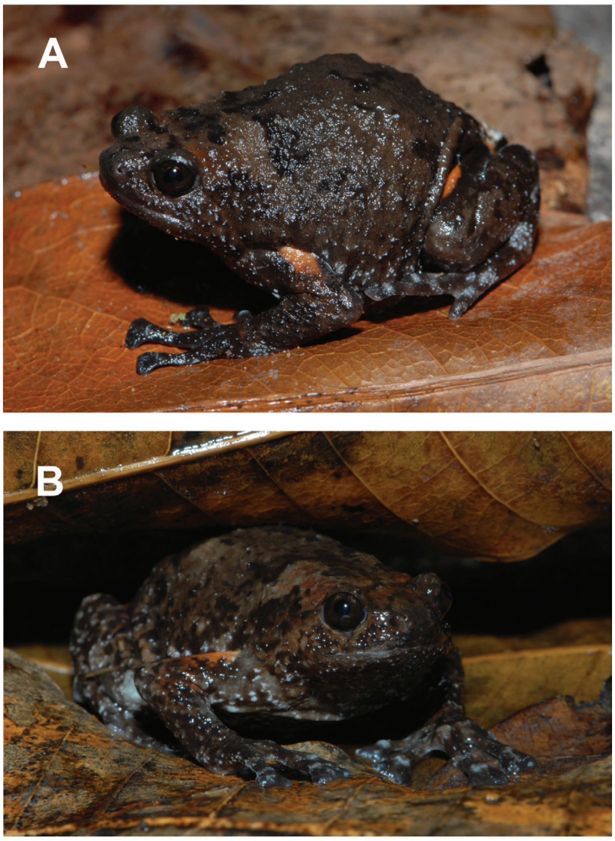

Figure 11. Dorsolateral (**A**) and frontal (**B**) views of the holotype of *Kaloula laosensis* sp. nov. in situ (ZISP 15284, male). Photographs by N.L. Orlov.

of the new species is shown in Fig. 5, and the locality information is detailed in Appendix 1. In Nakai-Nam Theun NP and in Hin Nam No NP, Khammouane Province, Laos, the new species was recorded from limestone evergreen tropical forests at relatively low elevations of ca. 100–300 m asl. The data on the natural history of *Kaloula laosensis* sp. nov. is scarce; it inhabits primarily lowland forests and is quite secretive, emerging only after heavy rains from June to September, when depressions in the forest floor are flooded and form temporary pools. The new species is likely associated with limestone karst landscapes of central Laos; the actual distribution of *Kaloula laosensis* sp. nov. is unknown, but we suppose that this species is likely to occur in adjacent provinces of Vietnam (Ha Tinh and Quang Binh), which harbor limestone forests similar in composition. Details about the new species' reproductive biology and diet are unknown.

Comparisons. *Kaloula laosensis* sp. nov. most closely resembles other members of the *K. baleata* species complex in overall morphology, and comparison with these species appears to be the most pertinent. Most specifically, the new species superficially resembles *K. indochinensis*, with which it was previously confused. From *K. indochinensis*, *Kaloula laosensis* sp. nov. can be distinguished by having relatively longer head in males (HL/SVL 0.24 [n = 1] by our data or mean 0.25 ± 0.1 [n = 4] reported by Chan et al. 2013) vs. mean 0.23 ± 0.1 [n = 18] by our data or [n = 25] reported by Chan et al. 2013); relatively wider disk of finger III in males (3FDD/HAL 0.26 ± 0.1 [n = 1] vs. mean 0.23 ± 0.1 [n = 18]); relatively longer first toe in males (1TOEL/FL 0.29 ± 0.1 [n = 1] vs. mean 0.26 ± 0.1 [n = 18]); by having three metacarpal tubercles with median metacarpal tubercle touching both the inner and outer metacarpal tubercles, see Fig. 9A (vs. median metacarpal tubercle small, not touching the inner metacarpal tubercle, see Fig. 9B); by having two subarticular tubercles on toe IV, see Fig. 9A (vs. three well-developed subarticular tubercles, see Fig. 9B); by having supranumerary tubercles at the basis of toes I, III, and IV, see Fig. 9A (vs. supranumerary tubercles absent, see Fig. 9B); by the presence of numerous contrasting black markings on dorsum (vs. absent or indistinct); and brownish dorsal coloration (vs. chocolate to dark grayish-brown).

From *K. baleata*, *Kaloula laosensis* sp. nov. can be distinguished by having a relatively larger distance between nares in males (IND/HW 0.21 [n = 1] by our data or [n = 6] reported by Chan et al. (2013) vs. 0.18 ± 0.1 [n = 10] reported by Chan et al. (2013)); wider finger III disks in males (3FDD 3.4 ± 0.1 mm [n = 1] by our data) or mean 3.1 ± 0.3 mm [n = 6] reported by Chan et al. (2013) vs. 1.7 ± 0.2 mm [n = 10] reported by Chan et al. (2013)); by having two subarticular tubercles on toe IV, see Fig. 9A (vs. three well-developed tubercles); and by having supranumerary tubercles at the basis of toes I, III, and IV, see Fig. 9A (vs. supranumerary tubercles absent).

From *K. latidisca*, *Kaloula laosensis* sp. nov. can be distinguished by having relatively shorter heads in males (HL/SVL 0.24 [n = 1] by our data or mean 0.25 ± 0.1 [n = 4] reported by Chan et al. (2013) vs. mean 0.27 ± 0.1 [n = 4] reported by Chan et al. (2014)); relatively smaller distance between eyes in males (IOD/HW 0.34 [n = 1] by our data or mean 0.33 ± 0.1 [n = 6] reported by Chan et al. (2013) vs. mean 0.30 ± 0.1 [n = 4] reported by Chan et al. ((2014); by the presence of numerous black markings on the dorsum (vs. black markings on dorsum absent or few); and by having two subarticular tubercles on toe IV (vs. three well-developed tubercles).

From *Kaloula discordia* sp. nov. (described above), the new species can be distinguished by having a relatively longer head in males (HL/SVL 0.24 [n = 1] by our data or mean 0.25 ± 0.2 [n = 6] reported by Chan et al. (2013) vs. mean 0.22 ± 0.2 [n = 14]); relatively shorter snout in males (SL/HL 0.43 [n = 1] by our data or mean 0.40 ± 0.1 [n = 6] reported by Chan et al. (2013) vs. mean 0.47 ± 0.1 [n = 14]); relatively narrower head in males (HW/HL 1.19 [n = 1] vs. mean 1.31 ± 0.2 [n = 14]); wider finger III disks (3FDD/HAL 0.26 [n = 1] vs. mean 0.23 ± 0.10 [n = 14]); shorter toe I (1TOEL/FL 0.29 [n = 1] vs. mean 0.25 ± 0.1 [n = 14]); by having three metacarpal tubercles, see Fig. 9A (vs. two metacarpal tubercles, see Fig. 9C); by having supranumerary tubercles at the basis of toes I, III, and IV, see Fig. 9A (vs. supranumerary tubercles absent, see Fig. 9C); by the brown coloration of the dorsum (vs. olive); and by the presence of numerous black markings on the dorsum (vs. black markings on dorsum absent or few).

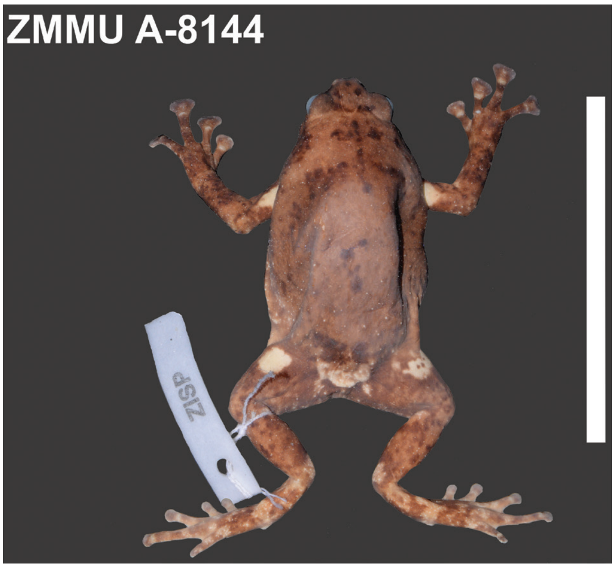

Figure 12. Dorsal coloration in a single paratype of *Kaloula laosensis* sp. nov. (ZMMU-A-8144, female) Scale bar equals 5 cm. Photograph by V.A. Gorin.

Furthermore, *Kaloula laosensis* sp. nov. differs from *K. aureata* by having a brownish dorsum with no reticulations (vs. golden dorsum with dark brown reticulations); from *K. borealis* by having wide finger disks (vs. finger tips dilated but not forming wide disks); by the absence of yellowish blotches on flanks (vs. present); an by brownish dorsal coloration (vs. gray-brown). *Kaloula laosensis* sp. nov. further differs from *K. conjuncta* by the stratified coloration on flanks absent (vs. present); by having distinct outer metatarsal tubercle (vs. weak or indistinct); from *K. ghoshi* by the presence of axillary and inguinal spots (vs. axillary and inguinal spots absent); by tuberculated dorsum and venter (vs. smooth or with small flat granules dorsally); by brownish dorsal coloration (vs. orange-brown). The new species differs from *K. kalingensis* in that it has tubercles on the dorsum (vs. dorsum smooth), a distinct outer metatarsal tubercle (vs. indistinct), and yellow or orange axillary and inguinal spots (vs. usually absent or small and red if present). *Kaloula laosensis* sp. nov. further differs from *K. kokacii* by the presence of dorsal tubercles, axillary and inguinal spots, and a light pericloacal ring (vs. absent). The new species differs from *K. mediolineata* by dorsolateral stripes and sacral stripe absent (vs. present); by having enlarged, wide finger disks (vs. finger tips slightly dilated but not forming wide disks); from *K. nonggangensis* by protuberant tubercles on the upper surface of finger tips absent (vs. present); from *K. picta* by the absence of dorsolateral stripes and stratified coloration on flanks (vs. present); by having enlarged, wide finger disks (vs. finger tips slightly dilated but not forming wide disks). The new species can be readily diagnosed from *K. pulchra* by the absence of dorsolateral stripes (vs. present) and by having axillary and inguinal spots (vs. absent). *Kaloula laosensis* sp. nov. further differs from *K. rigida* by having enlarged, wide finger disks (vs. finger tips slightly dilated but not forming wide disks), by the absence of dorsolateral stripes and stratified coloration on flanks (vs. present), and by having axillary and inguinal light spots (vs. absent). The new species differs from *K. rugifera* by having enlarged, wide finger disks (vs. slightly dilated small finger disks) and by having axillary and inguinal spots (vs. absent) and is further different from *K. verrucosa* by having very wide finger disks (vs. small finger disks) and by having axillary and inguinal spots (vs. absent). The new species differs from *K. walteri* by having very wide finger disks (vs. slightly dilated small finger disks), by the absence of stratified coloration on flanks (vs. presence), by having axillary and inguinal light spots (vs. absent), and by having a distinct outer metatarsal tubercle (vs. indistinct or absent). Except for *K. pulchra*, which can be found in central Laos in syntopy with the new species, *Kaloula laosensis* sp. nov. is geographically separated from most of its relatives.

Acoustic data. The male advertisement call of *Kaloula laosensis* sp. nov. has not been recorded, and the bioacoustic data on this species is absent.

Etymology. The specific epithet "*laosensis*" is an adjective in the nominative case, given in reference to the new species' distribution in central Laos. The name also mirrors the specific epithet of *K. indochinensis*, with which the new species was previously confused. We recommend "*Laotian Painted Frog*" as the common English name, "*Laosskiy bychiy uzkorot*" as the common name in Russian, "*Ễnh ương Lào*" as the common name in Vietnamese, and "ອຶງຢາງລາວ" ("*Ung Yang Lao*") as the common name in Lao languages.

Conservation status. At present, the new species is known only from two localities in Khammouane Province of Laos (Fig. 5). The main threats to this species in Laos are habitat loss and degradation due to intensified logging and deforestation, namely Nakai-Nam Theun NP and Hin Nam No NP. We propose that the IUCN's Red List categories (IUCN 2019) classify *Kaloula laosensis* sp. nov. as Data Deficient (DD) due to the absence of comprehensive studies in the adjacent territories.

Comments. We assume, based on the distribution of the new species, that several specimens from the type series of *K. indochinensis* in the original description by Chan et al. (2013), collected in Khammouance Province of Laos and labeled as '*K. indochinensis* Laos' or 'Laos OTU' throughout the text, actually represent *Kaloula laosensis* sp. nov. These specimens include six adult males stored in the Field Museum of Natural History (FMNH), Chicago, USA, under voucher numbers FMNH 270360–65. The lack of genetic information on these specimens in the original description of *K. indochinensis* prevented Chan et al. (2013) from recognizing their taxonomic distinctiveness.

Discussion

Until recently, *K. baleata* sensu lato was reported to inhabit a vast area in Southeast Asia, including territories of Indonesia, Malaysia, India, Thailand, Laos, and Vietnam (Blackburn et al. 2013; Chandramouli and Prasad 2018). This was until Blackburn et al. (2013), who published the first comprehensive phylogeny of the genus, revealed that

K. baleata is a complex of (presumably) cryptic species, which motivated morphological investigations and taxonomic revisions (Chan et al. 2013, 2014). Our discovery of *Kaloula discordia* sp. nov. from Southern Vietnam and *Kaloula laosensis* sp. nov. from Central Laos follows the recent descriptions of two new species from Indochina: *K. indochinensis* (see Chan et al. 2013) and *K. latidisca* (see Chan et al. 2014), as well as the elevation of *K. ghoshi* to full species status (see Chandramouli and Prasad 2018). It is quite remarkable that the populations from southern Vietnam and central Laos, which we herein describe as two new species, were well-known to the authors of previous taxonomic studies of this group (Chan et al. 2013, 2014). In fact, Chan et al. (2013) included six specimens from central Laos (FMNH 270360–65) in their morphological study, assigning them to *K. indochinensis* and including them in the type series of this species, but without assessing their genetic divergence from topotypic specimens of *K. indochinensis* from central Vietnam. Similarly, Chan et al. (2013) did not include specimens of the *K. baleata* complex members from southern Vietnam or adjacent Cambodia in their analysis. However, they included these localities in the proposed distribution range of '*K. indochinensis*,' likely based on photo records, likewise assuming their conspecificity. In essense, our study thus unravelled diversity in the *K. baleata* complex that was "hidden in plain sight" and thereby emphasized the need for careful genetic and phenotypic surveys in presumably widespread species of Southeast Asian amphibians. For example, the common practice of including specimens from different localities in a type series may be misleading. Here, the type locality of *K. indochinensis* described by Chan et al. (2013) from Gia Lai Province of Vietnam and the type locality of *Kaloula laosensis* sp. nov. in Central Laos are located in biogeographically and climatically different parts of Indochina, separated from each other by a straight distance of over 500 km (see Poyarkov et al. 2021b, 2023). Hence, including specimens from both areas in a type series without DNA-barcoding at least some representative specimens from each locality appears an unnecessary gamble.

Different research groups have developed a tradition of providing extensive datasets of morphological characters for Asian anurans (e.g., Poyarkov et al. 2014, 2020b, 2021a; Meegaskumbura et al. 2015; Garg et al. 2019; Biju et al. 2020; Suwannapoom et al. 2018; Brakels et al. 2023). However, some researchers continue to present limited datasets of seemingly handpicked morphological characters. In the description of *K. walteri* by Diesmos et al. (2002), authors provided data on a total of 21 morphometric characters, including complete measurements of fore- and hindlimbs. Mo et al. (2013) reduced the number of studied characters to 14 and lacked data on fingers, toes, and respective disks in their description of *K. nonggangensis*. In the description of *K. indochinensis* by Chan et al. (2013), the number of studied characters further decreased to 11, with no morphometric data on forelimbs and only partial data on hindlimbs. In the following paper, Chan et al. (2014) described *K. latidisca* and provided the same set of 11 characters. Finally, in the most recent taxonomic paper on the genus *Kaloula* (Chandramouli and Prasad 2018), the authors provided measurements on a set of 17 characters of *K. ghoshi*. None of the respective papers, however, explains or at least mentions the observed reduction in the number of studied morphometric characters. The lack of data on the morphology of these relatively newly described species makes it difficult to compare datasets from different studies and hampers further research into species diversity in *Kaloula* frogs (see the Morphology and Comparisons subsections in the Results section). Since amphibian taxonomy relies heavily on morphological descriptions, we emphasize the utmost importance of providing comprehensive and complete datasets for newly discovered and documented species that can then be re-used in future integrative studies.

Our discovery of two new species of the *K. baleata* complex from Indochina corroborates the idea that many species of Southeast Asian amphibians currently considered to be widely distributed may instead still encompass unrecognized diversity, hidden by a lack of comprehensive field surveys and/or the aforementioned deficiency of comprehensive morphological and genetic data (e.g., Chen et al. 2018; Hasan et al. 2019; Gorin et al. 2020; Suwannapoom et al. 2020; Poyarkov et al. 2020a; Lyu et al. 2023; Liu et al. 2024; Trofimets et al. 2024). Here, the new species of *Kaloula* from the Cat Tien National Park in southern Vietnam appears particularly remarkable. Cat Tien National Park covers one of the few remaining massifs of lowland monsoon forests in Vietnam and likely represents one of the best herpetologically studied areas in Vietnam (Yushchenko et al. 2023b). Herpetological exploration of this territory has continued for over 40 years with numerous expeditions and long-term monitoring programs by Vietnamese, Russian, German, USA, British, and Canadian herpetologists, the results of which were summarized in a monograph (Vassilieva et al. 2016). With 45 species of amphibians and 107 species of reptiles recorded in the park, Cat Tien NP is unanimously recognized as an important local center of herpetofaunal diversity (Geissler et al. 2011, 2015; Vassilieva et al. 2013, 2016; Holden and Poyarkov 2021; Yushchenko et al. 2023a,b). The new *Kaloula* species from Cat Tien NP thus illustrates the need for herpetological surveys even in presumably well-known Southeast Asian regions and species.

Moreover, our study provides new information on the evolution, diversity, and distribution of other members of the *K. baleata* species complex, specifically *K. latidisca* and *K. baleata*. Chan et al. (2014) described *K. latidisca* from Kedah, northern Peninsular Malaysia, based on phylogenetic data from Blackburn et al. (2013). In Chan et al.'s (2014) phylogenetic reconstruction, *K. latidisca* is suggested as a sister lineage to *K. baleata* sensu lato, which included samples from Java, Palawan, Borneo, Sulawesi, and southern Peninsular Malaysia. Chan et al. (2014) noted that the populations of southern Peninsular Malaysia and Borneo may not be conspecific with either *K. baleata* or *K. latidisca*, but they refrained from further taxonomic revisions and did not discuss the diversity and extent of distribution of members of the *K. baleata* complex in the

Thai-Malay Peninsula. First, our data showed relatively low, although species-level, sequence differentiation at the 16S rRNA gene between *K. latidisca* and the different lineages of *K. baleata* (p = 3.00%–3.96%; Table 2). Second, the monophyly of *K. baleata* with respect to *K. latidisca* is only moderately supported in our analyses (0.83/98, see Fig. 2). Finally, the mitochondrial distribution of *K. latidisca* and the three lineages of *K. baleata* partially overlap with each other, which requires investigating and potentially updating their respective ranges (see Fig. 1). Specifically, we hypothesize the following.

1. Our mitochondrial data suggests that *K. latidisca* inhabits southern peninsular Thailand, including Satun and Suratthani provinces (see Fig. 1); numerous localities of the *K. baleata* complex from the Isthmus of Kra in the north to the Thai-Malay national border in the south likely belong to this species, which is penetrating to Malaysia only in the state of Kedah (see Fig. 5).
2. The populations of the *K. baleata* complex from Tioman Island in southern Peninsular Malaysia, as well as from the Terengganu and Pahang states in northern Peninsular Malaysia, all belong to the *K. baleata* lineage 1 and thus appear conspecific with the populations from western Java based on their lack of mitochondrial differentiation. It appears that the Titiwangsa Mountain Range separates the *K. baleata* clade 1 and *K. latidisca* ranges in Peninsular Malaysia and southern Thailand.
3. The *K. baleata* population from the Tanintharyi Region of southern Myanmar features distinct mtDNA (lineage 3) that is genealogically closer to the mtDNA lineage(s) found in *K. baleata* sensu stricto (lineage 2) than to *K. latidisca* (Fig. 2). At the same time, this lineage likely extends to the Tenasserim Mountains/Tanintharyi Region north of the Isthmus of Kra (Figs 1, 5). This would imply that *K. latidisca* effectively separates the ranges of the *K. baleata* mtDNA lineages restricted to Sundaland and the Tenasserim Mountains north of the Isthmus of Kra.

These distribution patterns, combined with low genetic divergence in the 16S rRNA gene and unclear morphological differentiation between *K. latidisca* and *K. baleata*, stress the need for further integrative studies to clarify the distribution of these species and the taxonomic relevance of their mitochondrial diversity.

Our new data on the diversity and distribution in the *K. baleata* species complex may have important biogeographic implications. In eastern Indochina, the three *Kaloula* species (*K. indochinensis*, *Kaloula laosensis* sp. nov., and *Kaloula discordia* sp. nov.) group into a clade that is sister to the clade including all other populations of the complex, from the Thai-Malay Peninsula and Southeast Asian islands. The distribution areas of the three Indochinese species correspond well to the main biogeographic regions elaborated by Poyarkov et al. (2021b, 2023). Specifically, the range of *K. indochinensis* is associated with the Central Annamites region, while the newly described *Kaloula laosensis* sp. nov. and *Kaloula discordia* sp. nov. are restricted to the Northern Annamites and the Central-South Vietnam Lowlands, respectively. In the *K. baleata*-*K. latidisca* clade, the distribution of *K. baleata* lineage 1 encompasses Wallacea (Sulawesi, Sumba, and Palawan islands), Java, and Sumatra, while *K. baleata* lineage 2 extends over Borneo and eastern Peninsular Malaysia but also on Java (although it may be a result of a human-associated dispersal). At the same time, the range of *K. baleata* lineage 3 is restricted to the North Tenasserim Region, namely north of the Isthmus of Kra, while *K. latidisca* likely inhabits the South Tenasserim south of Kra and the South Thai-Malayan Lowlands Region. The diversification of these lineages and its association with paleographic events shall greatly benefit from phylogeographic analyses that implement nuclear markers, first to be able to assess their genomic divergence and to test for potential hybridization and introgression in areas of mitochondrial sharing.

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Appendix 1

Table A1. List of localities of the *Kaloula baleata* complex members in Indochina appearing on Fig. 5. **Symbols:** (1) = Locality number on Fig. 5; (2) = Verified by morphology data (yes/no); (3) = Verified by molecular data (yes/no).

Species	(1)	(2)	(3)	Location	Sources
K. laosensis sp. nov.	1	yes	yes	Nakai-Nam Theun NP, Khammouan, Laos (type locality)	Chan et al. (2013); our data
K. laosensis sp. nov.	2	yes	no	Hin Nam No NP, Khammouane, Laos	Luu et al. (2016)
K. indochinensis	3	yes	no	Kiat Ngong, Xepian NBCA, Champasak, Laos	Chan et al. (2013)
K. indochinensis	4	yes	no	Chu Mom Ray NP, Kon Tum, Vietnam	Jestrzemski et al. (2013)
K. indochinensis	5	yes	yes	Kon Chu Rang NR, Gia Lai, Vietnam (type locality)	Chan et al. (2013); our data
K. indochinensis	6	yes	yes	Kon Ka Kinh NP, Gia Lai, Vietnam	Vassilieva et al. (2016); our data
K. indochinensis	7	yes	no	An Khe, Gia Lai, Vietnam	Chan et al. (2013); our data
K. indochinensis	8	yes	no	Song Hinh, Phu Yen, Vietnam	Do et al. (2017)
K. indochinensis	9	yes	no	Tuy Hoa, Phu Yen, Vietnam	Do et al. (2017)
K. indochinensis	10	yes	yes	Yok Don NP, Dak Lak, Vietnam	our data
K. discordia sp. nov.	11	yes	yes	Phnum Prech WS, Mondulkiri, Cambodia	Chan et al. (2013)
K. discordia sp. nov.	12	yes	no	Bu Gia Map NP, Binh Phuoc, Vietnam	Vassilieva et al. (2016); our data
K. discordia sp. nov.	13	yes	yes	Bao Lam, Lam Dong, Vietnam	Vassilieva et al. (2016); https://www.inaturalist.org/observations/212830145
K. discordia sp. nov.	14	yes	yes	Cat Tien NP, Dong Nai, Vietnam (type locality)	our data; https://www.inaturalist.org/observations/168961087
K. discordia sp. nov.	15	yes	no	Lo Go-Xa Mat NP, Tay Ninh, Vetnam	Vassilieva et al. (2016); our data
K. baleata Clade 3	16	yes	no	Thungyai Naresuan East, Umphang, Tak, Thailand	our data
K. baleata Clade 3	17	yes	no	Thong Pha Phum, Kanchanaburi, Thailand	https://www.inaturalist.org/observations/180645435
K. baleata Clade 3	18	yes	no	Suan Phueng, Ratchaburi, Thailand	our data
K. baleata Clade 3	19	yes	no	Kaeng Krachan NP, Phetchaburi, Thailand	https://www.inaturalist.org/observations/153399059; https://www.inaturalist.org/observations/176926007
K. baleata Clade 3	20	no	yes	Yeybu, Tanintharyi, Myanmar	Zug et al. (2018)
K. baleata Clade 3	21	yes	no	Saphan, Prachuap Khiri Khan, Thailand	https://www.inaturalist.org/observations//218052579
K. latidisca	22	yes	no	Saeng, Surathani, Thailand	Chan-ard et al. (2011); our data
K. latidisca	23	yes	no	Khao Sok NP, Surat Thani, Thailand	https://www.inaturalist.org/observations/70379448; https://www.inaturalist.org/observations/191660698
K. latidisca	24	yes	yes	Kapong, Phangnga, Thailand	https://www.inaturalist.org/observations/161810790
K. latidisca	25	yes	no	Khao Lak-Lam Ru NP, Phang Nga, Thailand	Pauwels et al. (2000); https://www.inaturalist.org/observations/194115334
K. latidisca	26	yes	no	Thalang, Phuket, Thailand	https://www.inaturalist.org/observations/202954715
K. latidisca	27	yes	no	Khao Phanom Bencha NP, Krabi, Thailand	our data
K. latidisca	28	yes	no	Ban Na San, Surat Thabi, Thailand	https://www.inaturalist.org/observations/83178477
K. latidisca	29	yes	no	Tha Sala, Nakhon Si Thammarat, Thailand	https://www.inaturalist.org/observations/190990980
K. latidisca	30	yes	no	Khao Luang NP, Nakhon Si Thammarat, Thailand	Chan-ard et al. (2011); our data
K. latidisca	31	yes	no	Khao Pu-Khao Ya NP, Phatthalung, Thailand	https://www.inaturalist.org/observations/92061585
K. latidisca	32	yes	no	Namtok Khao Chong, Trang, Thailand	Chan-ard et al. (2011); our data
K. latidisca	33	yes	no	Yan Ta Khao, Trang, Thailand	https://www.inaturalist.org/observations/55886801
K. latidisca	34	yes	yes	Ton Nga Chang WS, Songkhla, Thailand	https://www.inaturalistchancc.org/observations/114582513
K. latidisca	35	yes	yes	Tha Le Ban NP, Satun, Thialnd	our data
K. latidisca	36	yes	no	Tarutao Island, Satun, Thialnd	Nidup et al. (2013); our data
K. latidisca	37	yes	no	Bang Lang NP, Yala, Thailand	https://www.inaturalist.org/observations/165320389
K. latidisca	38	yes	yes	Gubir, Kedah, Malaysia (type locality)	Chan et al. (2014)
K. baleata Clade 1	39	yes	yes	Kampung Merapunh Lama, Pahang, Malaysia	Chan et al. (2014)
K. baleata Clade 1	40	yes	no	Hulu Terengganu, Terengganu, Malaysia	Badli-Sham et al. (2023)
K. baleata Clade 1	41	yes	no	Kuala Tahan, Pahang, Malaysia	https://www.inaturalist.org/observations/116005614
K. baleata Clade 1	42	yes	yes	Tioman Island, Pahang, Malaysia	Grismer et al. (2006)