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The Phylogenetic Placement of Thai *Calotes* cf. *versicolor* (Squamata: Agamidae) within the Putative *Calotes irawadi* Species Complex

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ABSTRACT. – Since the restriction of *Calotes versicolor sensu stricto* to India, the status of *Calotes* cf. *versicolor* has been the subject of several taxonomic studies throughout its former distribution range, including Thailand. Among described species, *C. irawadi* is distributed from northeastern India to Vietnam. Based on subsequent studies, genetic variation obtained from limited set of samples suggested the potential existence of a species complex rather than a single taxonomic unit. *Calotes* cf. *versicolor* is commonly found in various habitats throughout Thailand. Therefore, the clarification of its taxonomic status is of importance. In this study, the degree of genetic variation among Thai *C.* cf. *versicolor* was investigated and compared to *C. irawadi* using the mitochondrial 16S rRNA gene (438 bp) to ascertain its position within the putative *C. irawadi* complex. DNA samples of *C.* cf. *versicolor* specimens from various regions of Thailand were examined. Based on the ML and BI phylogenetic trees, Thai *C.* cf. *versicolor* formed several closely related subclades, some of which shared the same subclade with *C. irawadi* from Myanmar and India. Substantial uncorrected *p*-distances (0.46–3.09%) were detected among Thai *C.* cf. *versicolor* suggesting the presence of several taxonomical units within the putative *C. irawadi* species complex.

KEYWORDS: *Calotes irawadi* complex, Thailand, 16S ribosomal RNA, phylogenetic tree, *p*-distance

INTRODUCTION

There are at least 30 nominal species within the genus *Calotes*, collectively distributed from South Asia to Southeast Asia and southern China, 12 of which have been reported from Indochina (Poyarkov et al., 2023; Uetz et al., 2024). Of these 12 species, the oriental garden lizard, *Calotes versicolor sensu lato* (Squamata: Agamidae), is distributed throughout South and Southeast Asia (Cox et al., 1998; Das and Das, 2018; Poyarkov et al., 2023), and is regarded as a species complex, comprising of multiple species, but characterized by subtle morphological differences (Dieckmann and Doebeli, 1999; Nosil, 2008; 2012).

Calotes versicolor sensu stricto is restricted to the Indian subcontinent (Gowande et al., 2021). Several nominal species have been described from the *C. versicolor* species complex, including *C. farooqi* Auffenberg & Rehman, 1995, *C. htunwini* Zug & Vindum, 2006, and *C. irawadi* Zug, Brown, Schulte & Vindum, 2006. In 2006, Zug et al. described *C. irawadi* from central Myanmar based on morphological and molecular data. Subsequently, Liu et al. (2021) reported the presence of *C. irawadi* in western Yunnan, China. Based on the phylogenetic analyses of 16S ribosomal RNA (16S rRNA) and cytochrome c oxidase subunit I (COI) sequences from Vietnam, Cambodia, and southern China, Gowande et al. (2021) hypothesized that *C.* cf. *versicolor* in Southeast Asia were monophyletic and embedded in a clade of *C. irawadi* from Myanmar and India. These samples, however, did not include specimens from the central part of Southeast Asia, specifically Thailand.

Among three *Calotes* species in Thailand, *C.* cf. *versicolor* is the most widespread (Chan-Ard et al., 2015) and has been the subject of several previous studies. Zug et al. (2006) compared and noted the morphological differences between *C. irawadi* and Thai *C.* cf. *versicolor* and made no taxonomic adjustments. Prakobkarn et al. (2016) noted on the morphological differences among *C.* cf. *versicolor* populations from northern and southern Thailand. More recently, Tantrawatpan et al. (2021) further revealed the genetic variation among populations on both sides of the Mekong River, which runs along the border of Thailand and Lao PDR. Despite numerous previous studies on the *C. versicolor* complex, the taxonomic status of *C.* cf. *versicolor* using genetic data in Thailand remains inconclusive. In this study, we investigated the degree of genetic variation among *C.* cf. *versicolor* populations in Thailand compared to samples of *C. irawadi* from Myanmar and India using the mitochondrial DNA and phylogenetic analyses.

MATERIALS AND METHODS

Molecular analyses

Tissue samples of *C.* cf. *versicolor* collected from various regions of Thailand were obtained from the herpetological collection of the Chulalongkorn

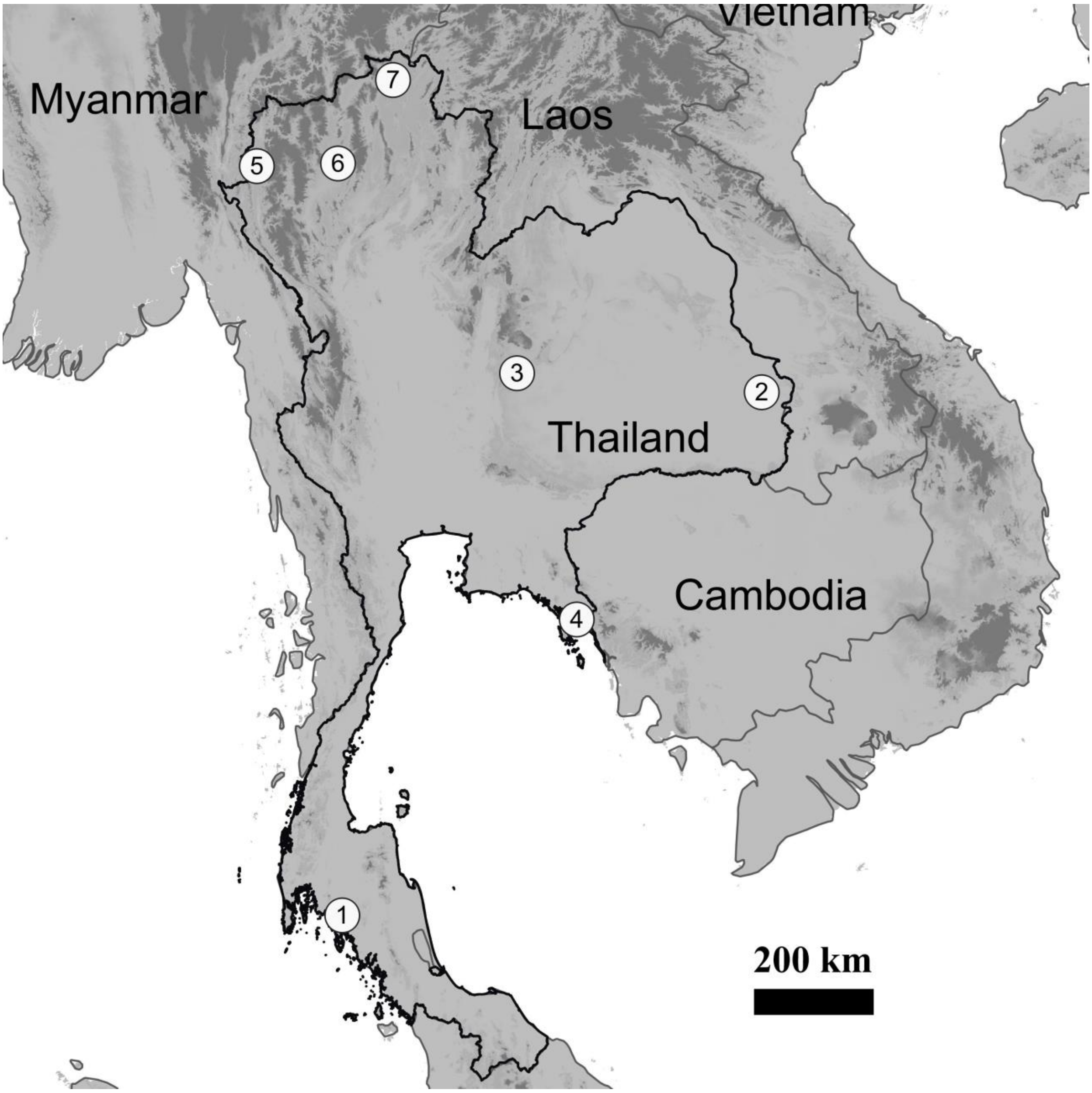

FIGURE 1. Localities of *Calotes* cf. *versicolor* samples (No. 1–7; see Table 1) from Thailand.

University Museum of Natural History, Bangkok, Thailand (Fig. 1 and Table 1). Genomic DNA were extracted from preserved liver or tail tissue using Biofact™ Genomic DNA Prep Kit (BIOFACT, Republic of Korea), following the protocol from the manufacturer. The mitochondrial 16S rRNA gene fragment was amplified by the polymerase chain reaction (PCR), using the 16Sar (5'-CGCCTGTTTATCAAAAACAT-3') and 16Sbr (5'-CTCCGGTTTGAACTCAGATCA-3') primers following Simon et al. (1991). PCR was performed under the following conditions: initial denaturation at 94 °C for 3 minutes, followed by 35 cycles of denaturation at 94 °C for 50 seconds, annealing at 52 °C for 1 minute, and extension at 72 °C for 40 second, and final extension at 72 °C for 5 minutes. PCR products were purified using the AccuPrep® PCR Purification Kit (Bioneer, Inc, Republic of Korea), following the manufacturer's protocol. Purified products were then sequenced using an ABI 3730XL automated DNA Sequencer. DNA sequences were edited and aligned using MEGA 11 (Tamura et al., 2021).

TABLE 1. Specimens of *Calotes* species included in the phylotgenetic analyses with their GenBank accession numbers.

No.	Species	Locality	Voucher Specimen No.	GenBank Accession No.	Source
1	*C.* cf. *versicolor*	Krabi, Thailand	CUMZ-R-2803	OR875332	This study
2	*C.* cf. *versicolor*	Ubon Ratchathani, Thailand	CUMZ-R-2845	OR875333	This study
3	*C.* cf. *versicolor*	Chaiyaphum, Thailand	CUMZ-R-2961	OR875334	This study
4	*C.* cf. *versicolor*	Trat, Thailand	CUMZ-R-2979	OR875335	This study
5	*C.* cf. *versicolor*	Mae Hong Son, Thailand	CUMZ-R-2825	OR875336	This study
6	*C.* cf. *versicolor*	Chiang Mai, Thailand	CUMZ-R-2812	OR875337	This study
7	*C.* cf. *versicolor*	Chiang Rai, Thailand	CUMZ-R-2992	OR875338	This study
8	*C. irawadi*	Sagaing, Myanmar	CAS 204862	MW901301	Gowande et al. (2021)
9	*C. irawadi*	Tripura, India	AG 855	MW901300	Gowande et al. (2021)
10	*C. irawadi*	Mizoram, India	MZMU2596	OL691119	Tariang et al. (2022)
11	*C. irawadi*	Mizoram, India	MZMU2385	OL691118	Tariang et al. (2022)
12	*C. irawadi*	Manipur, India	MZMU2230	ON041215	Decemson et al. (2023)
13	*C. versicolor*	Kerala, India	L190C	MH844730	Pal et al. (2018)
14	*C. versicolor*	Kerala, India	CESL 1086	MW901305	Gowande et al. (2021)
15	*C. emma*	Meghalaya, India	NCBSAQ	MH844707	Pal et al. (2018)
16	*C. emma*	Meghalaya, India	-	MK789847	Giri et al. (2019)
17	*C. calotes*	Tamil Nadu, India	CESL 1202	MW901254	Gowande et al. (2021)
18	*C. farooqi*	Punjab, Pakistan	CUDZ DJ 7902	MW901312	Gowande et al. (2021)
19	*C. vultuosu*	Chhattisgarh, India	NCBS ZM2	MW901281	Gowande et al. (2021)
20	*C. paulus*	Mizoram, India	-	MK789849	Giri et al. (2019)
21	*C. zolaiking*	India	-	MK789852	Giri et al. (2019)

All DNA sequences were manually checked and aligned using Molecular Evolutionary Genetic Analysis (MEGA) version 11 (Tamura et al., 2021). All sequences were deposited in GenBank under the accession numbers OR875332–OR875338 (Table 1). The sequences of closely related *Calotes* species were downloaded from GenBank database (Table 1) and included in the analyses. Phylogenetic trees were constructed using Maximum Likelihood (ML) and Bayesian Inference (BI) methods using IQ-TREE (Kalyaanamoorthy et al., 2017) and MrBayes (Ronquist et al., 2012). The evolution models were selected using ModelFinder function in IQ-TREE (Kalyaanamoorthy et al., 2017) with the Bayesian Information Criterion (BIC). All using IQ-TREE analyses were performed on the webserver (Trifinopoulos et al., 2016), with 1,000 bootstrap pseudo-replicates using the ultrafast bootstrap (UFB) approximation algorithm (Hoang et al., 2018). Nodes with UFB ≥ 95 were considered a strongly support (Minh et al., 2013). All MrBayes analyses were performed in version 3.2.6 (Ronquist et al., 2012) using the best-fitting substitution model in the program Kakusan4 (Tanabe, 2011) under BIC. The BI analyses were performed using Markov Chain Monte Carlo (MCMC) in runs for 100 million generations. Trees were sampled every 10,000 generations, and the first 25% of trees discarded as burn-in. Nodes with BPP ≥ 0.95 were strongly supported (Huelsenbeck and Rannala, 2004). Uncorrected pairwise sequence divergences (*p*-distance) of 16S were calculated in MEGA 11 (Tamura et al., 2021).

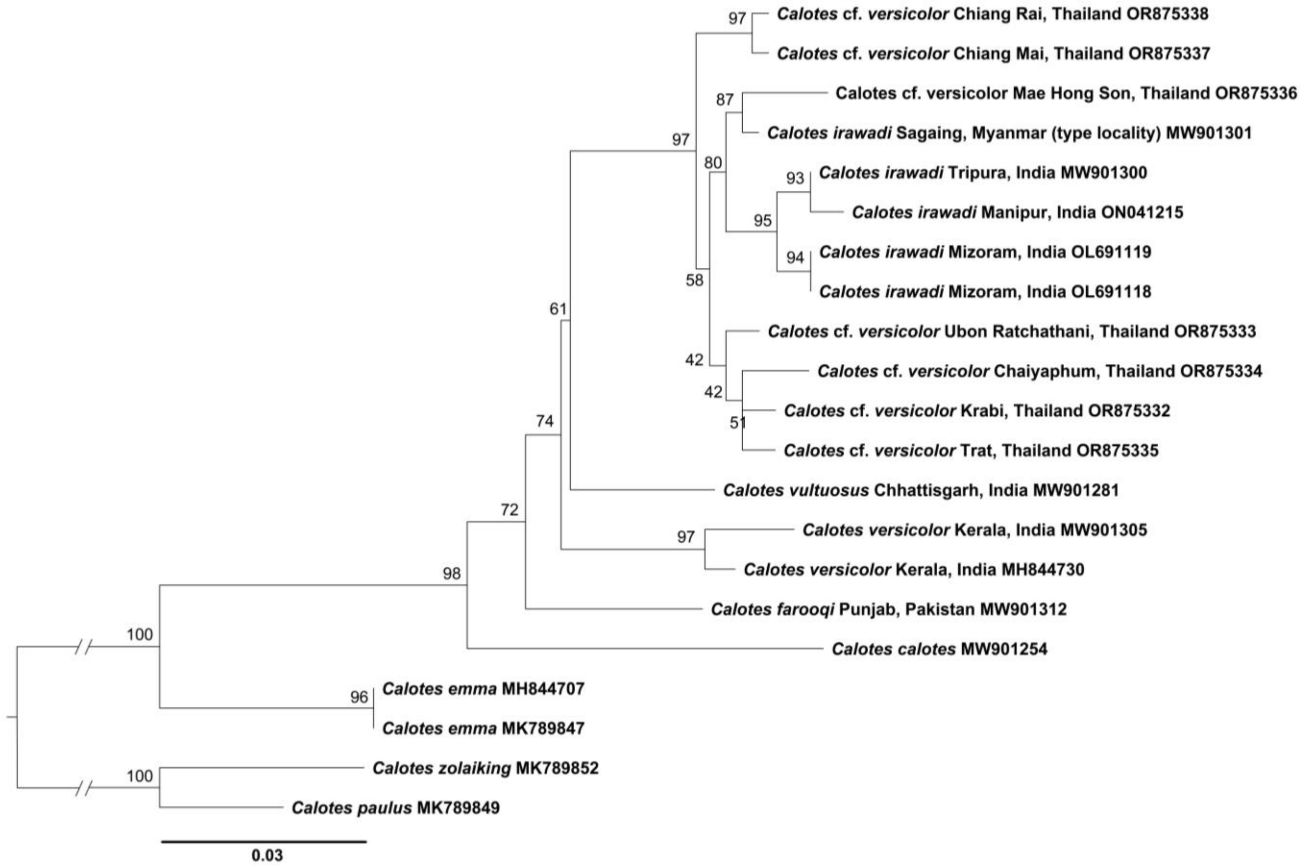

FIGURE 2. Phylogenetic relationships of *Calotes* species (N = 21) based on mitochondrial 16S rRNA partial sequences (438 bp). The phylogram is a Maximum Likelihood topology with Ultrafast ML Bootstrap (UFB) values and TIM2+F+I model.

Morphological analyses

Morphological characters, including number of midbody scales, number of dorsal scales, middorsal crest spine length, and supratympanic spine length, of Thai specimens were examined and compared with diagnostic characters of *C. irawadi* holotype from Sagaing, Myanmar and *C. versicolor* neotype from Pondicherry, India following Zug et al. (2006) and Gowande et al. (2016), respectively.

RESULTS

Based on the ML and BI phylogenetic trees, Thai *Calotes* cf. *versicolor* displayed a paraphyletic relationship, with close affinity, to *C. irawadi* from Myanmar and India with high support and was not grouped with *C. versicolor* clade (Fig. 2 and 3). All phylogenetic analyses revealed that *C. versicolor* sampled from Thailand had significant substructuring. Sample from Mae Hong Son grouped with the *C. irawadi* from Sagaing, Myanmar, while other Thai samples formed two clades within *C. irawadi*. (Figs. 2 and 3).

Among *C. irawadi* populations, *p*-distances between Myanmar (type locality) and India were 1.63–1.64% (Table 2). In Thailand, *p*-distances among *C.* cf. *versicolor* populations ranged from 0.46% to 3.09%. *Calotes irawadi* from Myanmar and India had *p*-distances that ranged from 1.17% to 1.88% and 1.88% to 3.08%, respectively. Comparatively, the interspecific *p*-distance between *C. paulus* and *C. zolaiking* was 4.06%, while the interspecific *p*-distance between *C. vultuosus* and *C. farooqi* was 4.31%. Notably, the interspecific *p*-distance between Thai *C.* cf. *versicolor* and *C. vultuosus* was 3.33–4.81% while the *p*-distance between *C. versicolor* and *C. irawadi* from India was 3.34–4.80%.

Based on the phylogenetic results, where Thai samples were grouped into three subclades (Fig. 2), some diagnostic characters were examined, the results of which are shown in Table 3. In general, all Thai *Calotes* cf. *versicolor* samples were morphologically

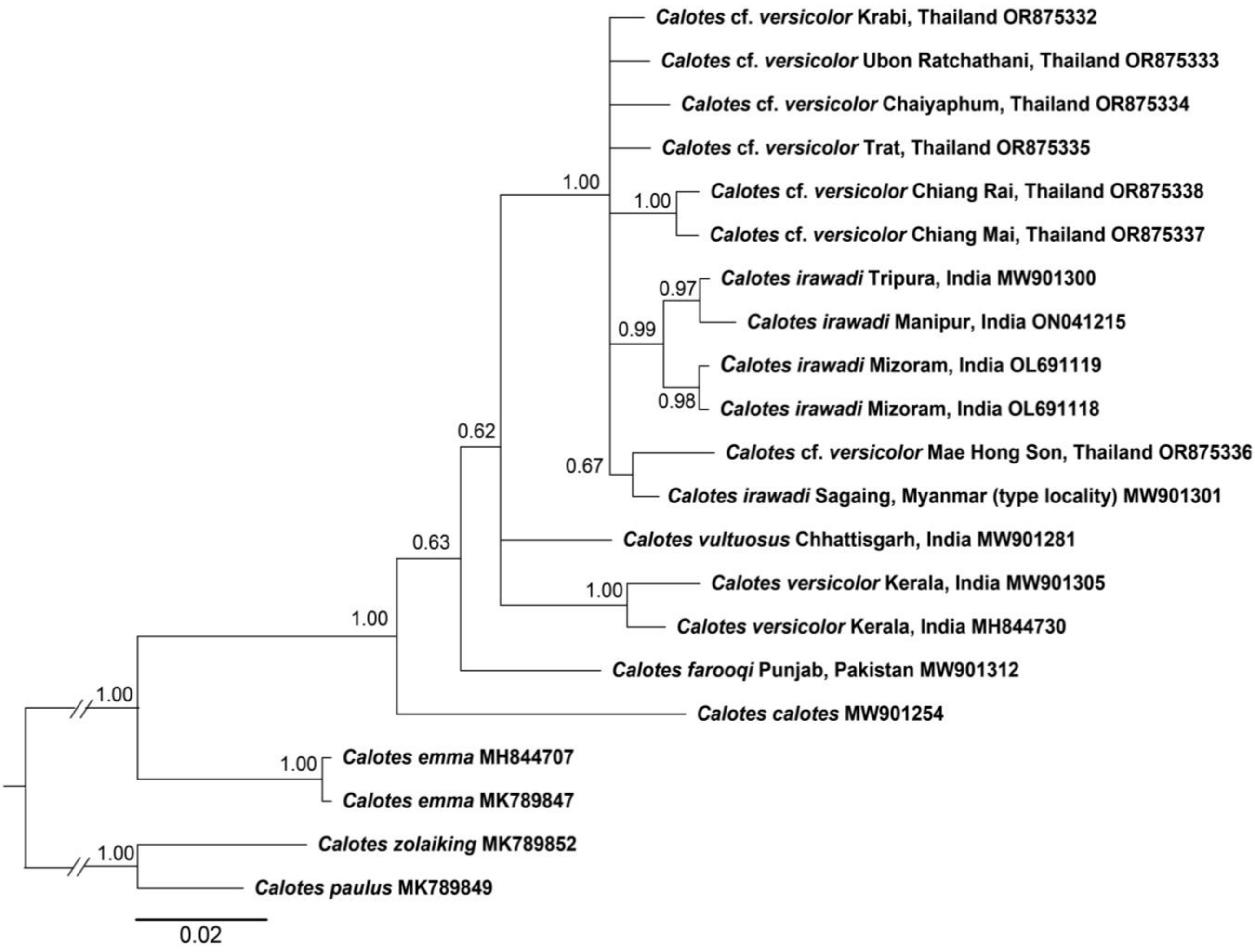

FIGURE 3. Phylogenetic relationships of *Calotes* species (N = 21) based on mitochondrial 16S rRNA partial sequences (438 bp). The phylogram is a Bayesian Inference (BI) topology with posterior probability (BPP) and GTR+G model.

distinct from *C. versicolor* neotype and *C. irawadi* holotype. Numbers of dorsal and midbody scales of Thai *Calotes* cf. *versicolor* samples were similar to *C. irawadi*. However, by comparison, male Thai *Calotes* cf. *versicolor* samples had relatively higher ratio of middorsal crest length per tympanum diameter and relatively higher ratio of supratympanic spine length per tympanum diameter.

DISCUSSION

The phylogenetic analyses of 16S rRNA sequences confirmed that Thai *C.* cf. *versicolor* are more closely related to *C. irawadi* from Myanmar and India. Subsequent to the taxonomic revisions of *C. versicolor sensu stricto* (Zug et al.,2006; Gowande et al., 2021), several species had been described from the former *C. versicolor* species complex, including *C. irawadi* from central Myanmar (Zug et al.,2006). The previously reported distribution of *C. irawadi* extended across Southeast Asia, including regions of Myanmar, Vietnam, Cambodia, southern China, and northeastern India, with possible existence of a species complex (Gowande et al., 2021; Tariang et al., 2021; Decemson et al., 2023). A recent description of a new species, *C. wangi* (Huang et al., 2023), from southern China and northern Vietnam, confirmed the presence of more than one species. The results from our study provided further supports and placed Thai samples within the *C. irawadi* species complex. indicating that there may be more unrecognized diversity.

TABLE 2. Average uncorrected pairwise distance (*p*-distance) within and between the *Calotes* species based on 438 bp of 16S rRNA gene. Ranges are showed in parentheses.

Taxon	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
1. *C.* cf. *versicolor*	**2.00**									
(Thailand; n=7)	**(0.46–3.09)**									
2. *C. irawadi*	1.64	**NA**								
(Myanmar; n=1)	(1.17–1.88)									
3. *C. irawadi*	2.54	1.64	**0.93**							
(India; n=3)	(1.88–3.08)	(1.63–1.64)	**(0.93–1.40)**							
4. *C. versicolor*	4.43	4.31	4.07	**1.64**						
(n=2)	(3.59–5.81)	(3.81–4.80)	(3.34–4.80)							
5. *C. vultuosus*	3.93	3.81	4.22	4.57	**NA**					
(n=1)	(3.33–4.81)		(4.05–4.30)	(4.31–4.82)						
6. *C. farooqi*	5.09	5.03	5.28	4.81	4.31	**NA**				
(n=1)	(4.81–5.30)		(5.04–5.53)	(4.56–5.06)						
7. *C. calotes*	7.45	7.3	7.74	6.99	6.84	5.82	**NA**			
(n=1)	(6.57–8.11)		(7.31–8.33)	(6.86–7.12)						
8. *C. emma*	7.74	7.17	7.51	8.25	7.42	8.45	9.97	**NA**		
(n=1)	(7.44–8.75)		(7.42–7.69)	(7.72–8.77)						
9. *C. paulus*	11.31	10.49	10.41	11.68	9.96	10.74	12.35	9.29	**NA**	
(n=1)	(10.80–11.89)		(10.24–10.51)	(11.68–11.69)						
10. *C. zolaiking*	12.23	11.71	11.37	12.66	10.38	11.43	13.86	10.15	4.06	**NA**
(n=1)	(11.76–12.85)		(11.20–11.47)	(12.65–12.67)						

In our study, the majority of the Thai samples were genetically distinct from each other. The *p*-distances between Thai *C.* cf. *versicolor* populations and *C. irawadi* from Myanmar and India were comparable to the interspecific *p*-distances observed between several described *Calotes* species, such as *C. irawadi* and *C. versicolor* (2.7–4.7%), *C. irawadi* and *C. vultuosus* (2.7–4.7%), *C. versicolor* and *C. vultuosus* (3.3–4.6%), and *C. irawadi* and *C. farooqi* (3.3–6.0%) (Gowande et al., 2021). The genetic distances from our study indicate that there could be the presence of separate taxonomical units within Thailand. Substantial population genetic structure based on COI sequences was also documented in *C.* cf. *versicolor* populations along the Mekong River in Thailand and Lao PDR (Tantrawatpan et al., 2021). Additionally, our phylogenetic analyses indicate that the samples from Mae Hong Son in northern Thailand, were closely affiliated with *C. irawadi* from Sagaing in Myanmar. This pattern is mirrored in species of *Leiolepis* and is the only place where *L. peguensis* from Myanmar can be found in Thailand (Promnun et al. 2021). Given this we hypothesize that Mae Hong Son Province could have a strong faunal influence from Myanmar.

The results of morphological analyses confirmed that Thai *C.* cf. *versicolor* are not only genetically distinct, but also morphologically different, compared *to C. irawadi* from Sagaing, Myanmar. Besides having relatively higher ratio of middorsal crest spine length per tympanum diameter (1.2x-1.28x) and relatively higher ratio of supratympanic spine length per tympanum diameter (0.5x-0.64x), Thai *C.* cf. *versicolor* has higher number of dorsal scales (47-60) compared to *C. irawadi*. This is inconsistent with Zug

TABLE 3. Comparison of morphological diagnostic characters between *Calotes* cf. *versicolor* from Thailand, *C. irawadi* (holotype) from Sagaing, Myanmar and *C. versicolor* (neotype) from Pondicherry, India.

Taxon	Locality	Voucher Specimen No.	Sex	Midbody scale	Dorsal scale	MCS/TymD	SSL/TymD
***C. versicolor* (Neotype)**[1]	Pondicherry, India	NCBS AT102	Male	42	36	N/A	N/A
***C. irawadi* (holotype)**[2]	Sagaing, Myanmar	USNM 520543	Male	48	49	1	0.25
C.* cf. *versicolor	Chiang Rai, Thailand	CUMZ-R-2992	Male	N/A	N/A	1.2	0.57
C.* cf. *versicolor	Chiang Mai, Thailand	CUMZ-R-2812	Female	45	59	1.08	0.36
C.* cf. *versicolor	Mae Hong Son, Thailand	CUMZ-R-2825	Male	42	48	1.27	0.5
C.* cf. *versicolor	Chaiyaphum, Thailand	CUMZ-R-2961	Male	N/A	N/A	1.28	0.64
C.* cf. *versicolor	Ubon Ratchathani, Thailand	CUMZ-R-2845	Female	46	52	1	0.38
C.* cf. *versicolor	Krabi, Thailand	CUMZ-R-2803	Female	45	60	0.75	0.44
C.* cf. *versicolor	Trat, Thailand	CUMZ-R-2979	Female	46	47	0.94	0.48

MCS/TymD = Middorsal crest spine length per tympanum diameter; SSL/TymD = Supratympanic spine length per tympanum diameter
[1] Data from Gowande et al. (2016); [2] Data from Zug et al. (2006)

et al. (2006), who noted that *C. irawadi* has higher number of dorsal scales, based on samples from Ubon Ratchathani, Thailand. In this study, however, examination of specimens collected from different regions of Thailand revealed higher variations in terms of number of dorsal scales. In addition, Prakobkarn et al. (2016) reported morphological differences between northern and southern populations. This suggests that there may be more unrecognized diversity within Thai *C.* cf. *versicolor*.

This study revealed distinct genetic differences between populations within the putative *C. irawadi* complex. We hypothesize that the substantial genetic distances and morphological differences are evidence of more than one species within this complex in Thailand. Further investigations involving larger sample sizes, multiple molecular makers, and detailed morphological examinations should be conducted to conclusively clarify the taxonomical status of *C.* cf. *versicolor* in Thailand and adjacent regions.

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