

**FIRST RECORD OF *Odorrana liboensis* Luo, Wang, Xiao, Wang & Zhou, 2021
(Amphibia: Anura: Ranidae) FROM VIETNAM**

Cuong The Pham^{1,2,✉}, Chung Van Hoang^{1,✉},
Thomas Ziegler^{3,4,✉}, Truong Quang Nguyen^{1,2,*✉}

¹Institute of Biology, Vietnam Academy of Science and Technology,
18 Hoang Quoc Viet, Ha Noi, Vietnam

²Graduate University of Science and Technology, Vietnam Academy of Science
and Technology, 18 Hoang Quoc Viet, Ha Noi, Vietnam.

³Cologne Zoo, Riehler Str. 173, D-50735 Cologne, Germany

⁴Institute of Zoology, University of Cologne, Zülpicher Str. 47b, D-50674 Cologne, Germany

Received 1 July 2025; accepted 10 December 2025

ABSTRACT

As a result of our fieldwork in Thai Nguyen and Lang Son provinces, we hereby record *Odorrana liboensis* Luo, Wang, Xiao, Wang & Zhou, 2021 for the first time from Vietnam. Morphologically, the newly collected specimens from Vietnam slightly differs from the type series from China by having a larger size (SVL 48.6–51.8 mm in males, SVL 61.4 mm in female vs. 47.1–49.9 mm in males, 55.8–58.2 mm in females) and by the absence of dorsolateral folds in adult females (vs. present). In terms of genetic divergence, the specimens from Vietnam differ from those from Guizhou province, China, by 0.14% to 0.70% based on the 16S rRNA fragment. Our finding increases the number of *Odorrana* species recorded in Vietnam to 24.

Keywords: *Odorrana*, genetic divergence, morphology, new record.

Citation: Cuong The Pham, Chung Van Hoang, Thomas Ziegler, Truong Quang Nguyen, 2025. First record of *Odorrana liboensis* Luo, Wang, Xiao, Wang & Zhou, 2021 (Amphibia: Anura: Ranidae) from Vietnam. *Academia Journal of Biology*, 47(4): 1–10. <https://doi.org/10.15625/2615-9023/23104>

*Corresponding author email: nqt2@yahoo.com

INTRODUCTION

Cascade frogs of the genus *Odorrana* have a wide distribution in Asia, from northeastern India and southern China eastwards to Japan, throughout Indochina and southwards to Sumatra and Borneo (Frost, 2025). The genus belongs to one of the most diverse groups of amphibians with 66 recognized species, and more than 15 new species have been described in the last ten years (Frost, 2025). Due to morphological similarity within the genus, species that were formerly thought to be widespread are now being recognized as complexes of species with much narrower distributions (Wang et al., 2015; Song et al., 2023; Chen et al., 2024; Li et al., 2024). In Vietnam, Pham et al. (2016b) described a new species, *Odorrana mutschmanni* Pham, Nguyen, Le, Bonkowski & Ziegler, 2016, from Cao Bang province. Pham et al. (2016a, 2020) also reported two new country records from Vietnam, namely *Odorrana lipuensis* Mo, Chen, Wu, Zhang & Zhou, 2015 and *Odorrana fengkaiensis* Wang, Lau, Yang, Chen, Liu, Pang & Liu, 2015.

The Libo Odorous Frog, *O. liboensis* Luo, Wang, Xiao, Wang & Zhou, 2021, was recently described from the limestone karst forest of Maolan National Nature Reserve, Libo County, Guizhou province, China (Luo et al., 2021). During our field surveys in northern Vietnam, several frogs were collected in limestone karst forests of Bac Kan (now Thai Nguyen) and Lang Son provinces. Closer morphological examination and molecular analysis showed that they are representatives of *Odorrana liboensis*, and we therefore report the species for the first time from Vietnam.

MATERIALS AND METHODS

Field surveys were conducted in Trang Dinh forest, Lang Son province in April 2019; in Ba Be National Park, Thai Nguyen province (formerly Bac Kan province) in March 2021 (Fig. 1). Frogs were collected between 19:00 and 23:00 h. After taking photographs in life, frogs were anaesthetized and euthanized in a closed vessel with a piece of cotton wool containing ethyl acetate (Simmons, 2002),

fixed in 80% ethanol for five hours, and later transferred to 70% ethanol for permanent storage. Tissue samples were preserved separately in 70% ethanol prior to fixation. Voucher specimens referred to in this paper were deposited in the collections of the Institute of Biology (IB, formerly known as Institute of Ecology and Biological Resources, IEBR), Ha Noi, Vietnam.

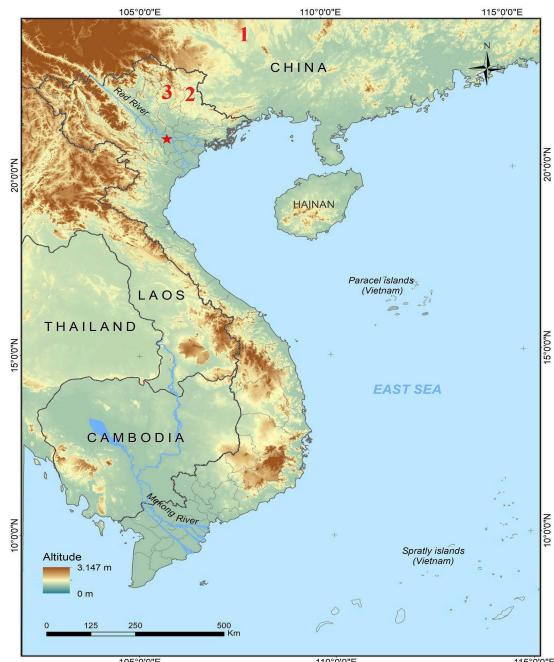


Figure 1. Map showing the type locality of *liboensis* in Guizhou province, China (1) and newly recorded localities in Vietnam: Trang Dinh forest, Lang Son province (2), Ba Be National Park, Thai Nguyen province (3)

Morphological characters: Measurements were taken with a digital caliper to the nearest 0.1 mm (Pham et al., 2016b; Luo et al., 2021). Abbreviations are as follows: SVL: snout-vent length, HL: head length (from the back of mandible to tip of snout), HW: maximum head width (across angle of jaws), RL: rostral length (from anterior corner of orbit to tip of snout), ED: eye diameter, UEW: maximum width of upper eyelid, IND: internarial distance, IOD: interorbital distance, DAE: distance between anterior corners of eyes, DPE: distance between

posterior corners of eyes, NS: distance from nostril to the tip of snout, EN: distance from anterior corner of eye to the nostril, TD: tympanum diameter, TYE: distance from anterior margin of tympanum to posterior corner of the eye, UAL: upper arm length (from axilla to elbow), FAL: fore arm length (from elbow to tip of third finger), TFL: third finger length, fd3: width of disc of finger III, IPT: inner palmar tubercle length, OPT: outer palmar tubercle length, NPL: nuptial pad length - finger I, FeL: femur length (from vent to knee), TbL: tibia length (from knee to tarsus), TbW: tibia width, FOL: foot length (from tarsus to the tip of fourth toe), FTL: fourth toe length, IMT: inner metatarsal tubercle length, td4: width of disc of toe IV. For the webbing formula, we followed Glaw & Vences (2007). Sex was determined by the presence of nuptial pads and based on gonadal inspection.

Molecular analysis: Two newly collected tissue samples of *Odorrana* were amplified ~560 base pairs length fragment of the 16S rRNA mitochondrial gene. Tissue samples were extracted using PureLinkTM RNA Micro Scale Kit (Thermo Fisher Scientific company), following the manufacturer's instructions. Total DNA was amplified using PCR Applied Biosystems. PCR volume consisted of 25 μ L, including 12 μ L of Master Mix, 6 μ L of water, 1 μ L of each primer at a concentration of 10 pmol/ μ L, and 5 μ L of DNA. Primers used in PCR and sequencing were as follows: LR-N-13398 (5'-CGCCTGTTACCAAAACAT-3'; forward) and LR-J 12887 (5'-CCGGTCT GAACTCAGATCACGT -3'; reverse) (Simon et al., 1994). PCR conditions: 94 °C for 5 minutes of initial denaturation; with 35 cycles of denaturation at 94 °C for 30 s, annealing at 56 °C for 30 s, and extension at 72 °C for 45 s; and the final extension at 72 °C for 7 minutes. PCR products were sent to Apical Scientific company for sequencing (<https://apicalscientific.com>). The obtained sequences were deposited in GenBank under the accession numbers PV523532 and PV523533.

In addition to the two new sequences of *Odorrana* from Vietnam, we used 14 available sequences (16S rRNA gene) of the limestone karst-restricted odorous frog group from GenBank for phylogenetic analyses. Sequences of *Rana weiningensis* were included in the analysis as an outgroup (Lin et al., 2022). Locality information and accession numbers for all sequences included in the analysis can be found in Table 1.

Chromas Pro software (Technelysium Pty Ltd., Tewantin, Australia) was used to edit the sequences, which were aligned using the ClustalW (Thompson et al., 1997) option in MEGA11 (Tamura et al., 2021) with default parameters and subsequently optimized manually in BioEdit 7.0.5.2 (Hall, 1999). We then checked the initial alignments by eye and adjusted them slightly to minimize gaps. Pairwise comparisons of uncorrected sequence divergences (p-distance) were calculated with MEGA11 (Tamura et al., 2021), where the outgroup was excluded.

Variances were estimated using a bootstrap method with 1,000 replicates using nucleotide substitution, while gaps/missing data were treated as pairwise deletions. Maximum likelihood phylogenies were inferred using IQ-TREE (Nguyen et al., 2015) under the GTR+R4+F model for 1,000 ultrafast bootstraps replicates (Minh et al., 2013), as well as the Shimodaira-Hasegawa-like approximate likelihood-ratio test (Guindon et al., 2010).

In the Bayesian Inference (BI) analysis, the parameters for each partition were unlinked, and branch lengths were allowed to vary proportionately across partitions. BI phylogenies were inferred using MrBayes 3.2.6 (Ronquist et al., 2012) under the JC+F model (2 parallel runs, 10,000,000 generations), in which the initial 25% of sampled data were discarded as burn-in, followed by calculations of Bayesian posterior probabilities and the 50% majority-rule consensus of the post-burn-in trees sampled at stationarity.

We checked parameter estimates and convergence using TRACER version 1.7.1 (Rambaut et al., 2018). We considered Bayesian posterior probability (BPP) and ultrafast bootstrap (UFB) support values of greater than or equal to 0.95 to indicate strong support (Felsenstein, 1985; Hoang et al., 2018).

RESULTS

Molecular phylogenetic analysis

The phylogenetic analysis included 15 sequences of 16S rRNA for limestone karst-restricted odorous frogs. Among 473 nucleotide positions, 394 sites were conserved and 79 sites were variable, of which 58 were found to be potentially

parsimony-informative. Evolutionary analyses were conducted in MEGA11 (Tamura et al., 2021). The estimated transition/transversion bias (R) is 3.964. Substitution patterns and rates were estimated under the Tamura (1992) model. The nucleotide frequencies were A = 31.35%, T/U = 22.75%, C = 25.67%, and G = 20.23%. Phylogenetic analyses employing ML and BI were nearly identical, with most well supported nodes on the ML tree also well supported on the Bayesian tree, and only the BI tree is presented (Fig. 2). In both analyses, the two newly collected samples and the paratype of *Odorrana liboensis* (GZNU20180608003, GenBank accession number MW481352) were recovered as a closely related monophyletic group (Fig. 2).

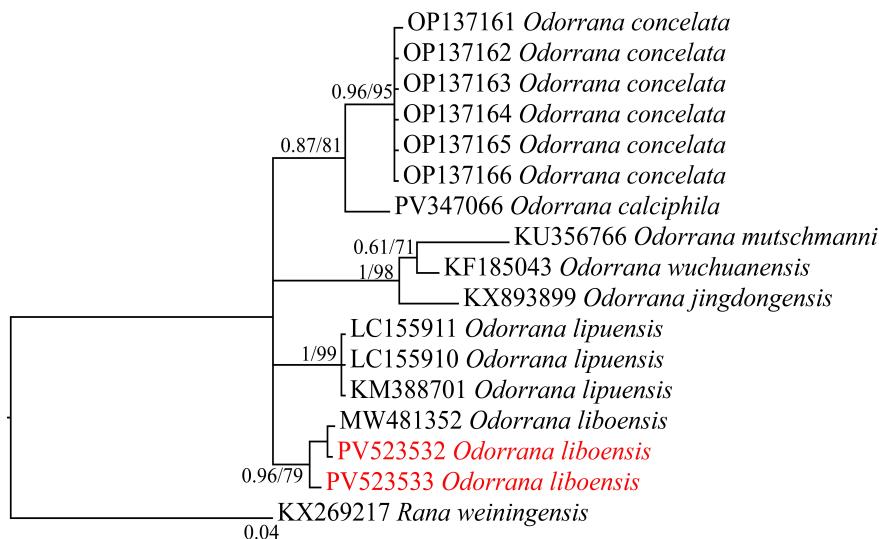


Figure 2. Bayesian phylogram of *Odorrana liboensis* and related taxa from northern Vietnam and southern China based on a partial 16S mitochondrial fragment. Numbers above and below branches are MP/ML bootstrap values and Bayesian posterior probabilities (> 50%), respectively

In this study, we also compare genetic distances between the newly recorded species from Vietnam and other limestone karst-restricted odorous frogs known from China (i.e., *Odorrana lipuensis* Mo, Chen, Wu, Zhang & Zhou, 2015; *Odorrana concelata* Wang, Zeng & Lin, 2022; and *Odorrana calciphila* Song, Qi, Wang, Liu & Wang, 2025) (see Mo et al., 2025; Lin et al., 2022; Song et al., 2025). Interspecific

uncorrected p-distances of the limestone karst-restricted odorous frogs (Table 1) ranged from 2.14% (between *Odorrana jingdongensis* & *Odorrana wuchuanensis*) to 7.42% (between *Odorrana jingdongensis* & *Odorrana concelata*). The genetic divergence between the two newly collected samples and the paratype of *O. liboensis* ranged from 0.14% (PV523533) to 0.70% (PV523532) (Table 1).

Table 1. Interspecific uncorrected p-distance of *Odorrana liboensis* and the limestone karst-restricted odorous frogs

No.	Sample	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	PV523532 <i>Odorrana liboensis</i>															
2	PV523533 <i>Odorrana liboensis</i>	0.56														
3	MW481352 <i>Odorrana liboensis</i>	0.70	0.14													
4	LC155911 <i>Odorrana lipuensis</i>	2.90	3.05	3.04												
5	LC155910 <i>Odorrana lipuensis</i>	2.90	3.05	3.04	0.00											
6	KM388701 <i>Odorrana lipuensis</i>	2.90	3.05	3.04	0.00	0.00										
7	KX893899 <i>Odorrana jingdongensis</i>	4.95	5.42	5.25	6.07	6.07	6.07									
8	KU356766 <i>Odorrana mutschmanni</i>	5.77	6.25	6.07	6.91	6.91	6.91	4.07								
9	KF185043 <i>Odorrana wuchuanensis</i>	4.50	4.97	4.80	5.29	5.29	5.29	2.14	2.88							
10	OP137161 <i>Odorrana conceleata</i>	4.46	4.61	4.44	4.43	4.43	4.43	7.24	7.42	6.94						
11	OP137162 <i>Odorrana conceleata</i>	4.30	4.45	4.28	4.28	4.28	4.28	7.07	7.26	6.77	0.14					
12	OP137163 <i>Odorrana conceleata</i>	4.30	4.45	4.28	4.28	4.28	4.28	7.07	7.26	6.77	0.14	0.00				
13	OP137164 <i>Odorrana conceleata</i>	4.30	4.45	4.28	4.28	4.28	4.28	7.07	7.26	6.77	0.14	0.00	0.00			
14	OP137165 <i>Odorrana conceleata</i>	4.30	4.45	4.28	4.28	4.28	4.28	7.07	7.26	6.77	0.14	0.00	0.00	0.00		
15	OP137166 <i>Odorrana conceleata</i>	4.30	4.45	4.28	4.28	4.28	4.28	7.07	7.26	6.77	0.14	0.00	0.00	0.00	0.00	
16	PV347066 <i>Odorrana calciphila</i>	4.08	4.55	4.38	4.53	4.53	4.53	6.55	7.25	6.25	2.50	2.34	2.34	2.34	2.34	2.34

Description of *Odorrana liboensis* Luo, Wang, Xiao, Wang & Zhou, 2021 from Vietnam

***Libo Odorous Frog/Éch dá libo* (Figs. 3, 4 & Table 2)**

Specimens examined (n = 3). One adult male (IEBR A.5207) collected by T. Q. Phan, H. N. Ngo & H. Q. Nguyen on 5 April 2019, in the karst forest (22°21.239'N, 106°25.109'E, at an elevation of 391 m), Trang Dinh forest, Lang Son province; one male (IEBR A.5210) and one female (IEBR A.5211) collected by C. V. Hoang on 20 March 2021 in the karst forest (22°25.481'N, 105°35.088'E, at an elevation of 730 m), Ba Be National Park, Thai Nguyen province.

Description. Morphological characters of specimens from Thai Nguyen and Lang Son provinces agreed well with the description of Luo et al. (2021). Size medium (SVL 48.6–51.8 mm, n = 2 in males, SVL 61.4 mm, n = 1 in female); head longer than wide (HL/HW 1.12–1.14, in males, HL/HW 1.13 mm in female); snout round in dorsal view, projecting beyond lower jaw; nostril lateral, closer to tip of snout than to eye (NS/EN 0.70–0.77 in males, NS/EN 0.80 in female); canthus rostralis distinct; pupil horizontally oval; loreal region slightly concave and oblique; snout length greater than eye diameter (ED/RL 0.86–0.93 in males, ED/RL 0.84 in female); interorbital distance wider than internarial

distance and upper eyelid (IOD 5.1–5.8 mm, IND 4.9–5.1 mm, UEW 4.0–4.4 mm in males; IOD 5.9 mm, IND 5.8 mm, UEW 4.8 mm in female); tympanum distinct, round, smaller than eye diameter (TD/ED 0.67–0.69 in males, TD/ED 0.65 in female); vomerine teeth present, in two oblique ridges; tongue cordiform, deeply notched posteriorly.

Forelimbs robust, upper arm length (UAL 10.5–12.0 mm in males, 13.8 mm in female) shorter than forearm length (FAL 23.8–26.4 mm in males, 31.5 mm in female); fingers free of webbing, relative finger lengths I < II < IV < III; tips of fingers expanded into discs; subarticular tubercles present, formula 1, 1, 2, 2; palmar tubercles prominent, round; inner and outer metatarsal present; nuptial pad on finger I present in males.

Hindlimbs long, thigh shorter than tibia (FeL 25.6–26.3 mm, Tbl 27.8–28.9 mm in males; FeL 29.9 mm, TbL 33.4 mm in female); tibia approximately five times longer than wide (TbL/TbW 5.0–5.1 in males, TbL/TbW 5.2 in female); tips of toes round, expanded into discs; relative toe lengths I < II < III < V < IV; webbing well developed, formula I0–1/2II0–1/2III0–1/2VII1/2–0V; subarticular tubercles present, formula 1, 1, 2, 3, 2; inner metatarsal tubercle elongate; outer metatarsal tubercle absent; tibio-tarsal articulation reaching to between eye and nostril when hindlimb adpressed along body.



Figure 3. Odorrana liboensis (IEBR A.5207, male) from Lang Son province:
A) dorsolateral view, B) ventral view

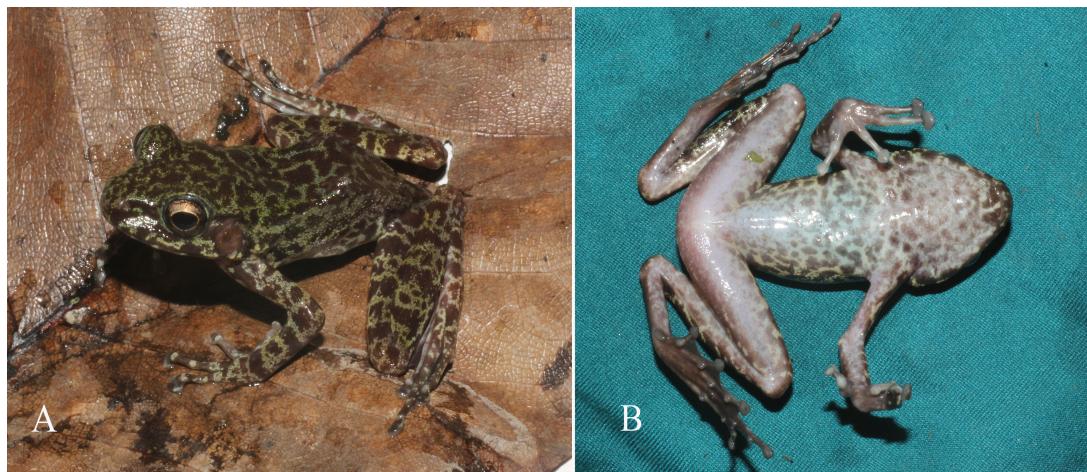


Figure 4. *Odorrana liboensis* (IEBR A.5211, female) from Thai Nguyen province: A) dorsolateral view, B) ventral view

Table 2. Measurements (in mm) and proportions of the newly collected specimens of *Odorrana liboensis* from Vietnam (M = Male, F = Female; for other abbreviations see Materials and methods)

Measurement	IEBR A.5207	IEBR A.5210	IEBR A.5211	Measurement and proportion	IEBR A.5207	IEBR A.5210	IEBR A.5211
Sex	M	M	F	Sex	M	M	F
SVL	51.8	48.6	61.4	OPT	2.1	2.3	2.8
AG	22.6	20.7	28.8	fd3	2.1	1.8	2.6
HL	16.3	15.6	21.1	FeL	26.3	25.6	29.9
HW	1.6	17.5	23.8	TbL	28.9	27.8	33.4
MN	15.8	14.9	20.2	TbW	5.8	5.5	6.4
MFE	13.5	11.4	15.9	FoL	38.5	36.9	43.9
MBE	7.9	6.7	9.8	fd4	1.8	1.3	2.0
RL	6.9	7.3	9.7	IMT	2.6	2.3	3.2
ED	6.4	6.3	8.1	HL/SVL	0.36	0.36	0.39
NS	3.0	3.0	4.3	HW/SVL	0.31	0.32	0.34
EN	3.9	4.3	5.4	HL/HW	1.14	1.12	1.13
TD	4.4	4.2	5.3	TYD/ED	0.69	0.67	0.65
TYE	2.1	1.7	2.6	ED/TD	1.45	1.50	1.53
UEW	4.4	4.0	4.8	ED/RL	0.93	0.86	0.84
IOD	5.8	5.2	5.9	SL/HL	0.37	0.42	0.41
IND	5.1	4.9	5.8	NS/EN	0.77	0.70	0.80
DAE	8.1	7.9	9.8	IOD/UEW	1.32	1.30	1.23
DPE	12.5	12.3	15.2	FeL/SVL	0.51	0.53	0.49
UAL	12.0	10.5	13.8	UAL/SVL	0.23	0.22	0.22
FAL	26.4	23.8	31.5	FAL/SVL	0.51	0.49	0.51
NPL	4.9	4.2		FoL/SVL	0.74	0.76	0.71
IPT	3.6	3.1	4.0	TbL/SVL	0.56	0.57	0.54

Skin: Dorsal surface of head and body smooth; flanks with tubercles; tiny spinules on upper edge of eyelid, anterior and posterior edge of tympanum; supratympanic fold weakly

developed; dorsolateral conical spines absent; dorsolateral fold absent; dorsal surface of limbs smooth; throat, chest, belly and ventral surface of thigh smooth.

Coloration in life: Iris black, surrounded by a golden network; dorsal surface of head and body green with brown mottling, brown patterns larger posteriorly; flank pale green with brown spots; dorsal surface of fore and hindlimbs green with brown cross bands; upper lip with brown bars; throat, chest and belly cream with dark brown mottling; underside of thigh cream.

Ecological notes: Specimens were found between 19:00 and 23:00 on the rocks or on the ground in rocky streams. The surrounding habitat was a mixed secondary karst forest of medium and small hardwoods and shrubs.

DISCUSSION

The specimens from Vietnam differ from the type series from China by having a slightly larger size (SVL 48.6–51.8 mm in males, SVL 61.4 mm in female vs. 47.1–49.9 mm in males, 55.8–58.2 mm in females) and by the absence of dorsolateral folds in adult females (vs. present). The specimen from Lang Son province was found at an elevation of 391 m a.s.l., lower than the known altitudinal range of the species in Maolan National Nature Reserve, Libo County, Guizhou province, China (645–728 m a.s.l.) (Luo et al., 2021). The geographical distance between the two populations of *Odorrana liboensis* recorded in Lang Son and Thai Nguyen provinces is about 86 km, and the distance from the type locality in China is approximately 380 km.

The genetic distance between the *Odorrana liboensis* populations in Vietnam and China was negligible, ranging from 0.14% to 0.70%. The genetic distance between the populations of *Odorrana liboensis* from Lang Son and Thai Nguyen was 0.56%. The genetic distance between the two species, *Odorrana liboensis* and *O. lipuensis*, in Vietnam ranged from 2.90% to 3.05% (Table 1). These findings suggest complex evolutionary isolation not only between the two species but also among

populations within each species. This evolutionary isolation appears to be independent of geographical distance. Further studies on the evolutionary ecology of this species group are needed to clarify the factors driving their evolutionary trajectories.

Our finding brings the total species number of the genus *Odorrana* to 24 in Vietnam, namely *Odorrana absita* (Stuart & Chan-ard); *Odorrana bacboensis* (Bain, Lathrop, Murphy, Orlov & Ho); *Odorrana banaorum* (Bain, Lathrop, Murphy, Orlov & Ho); *Odorrana chapaensis* (Bourret); *Odorrana chloronota* (Günther); *Odorrana fengkaiensis* Wang, Lau, Yang, Chen, Liu, Pang & Liu; *Odorrana geminata* Bain, Stuart, Nguyen, Che & Rao; *Odorrana gigatympana* Orlov, Ananjeva & Ho; *Odorrana grahami* (Boulenger); *Odorrana graminea* (Boulenger); *Odorrana jingdongensis* Fei, Ye & Li; *Odorrana junlianensis* Huang, Fei & Ye; *Odorrana khalam* (Stuart, Orlov & Chan-ard); *Odorrana liboensis* Luo, Wang, Xiao, Wang & Zhou; *Odorrana lipuensis* Mo, Chen, Wu, Zhang & Zhou; *Odorrana margaretae* (Liu); *Odorrana morafkai* (Bain, Lathrop, Murphy, Orlov & Ho); *Odorrana mutschmanni* Pham, Nguyen, Le, Bonkowski & Ziegler; *Odorrana nasica* (Boulenger); *Odorrana orba* (Stuart & Bain); *Odorrana tiannanensis* (Yang & Li); *Odorrana trankieni* (Orlov, Le & Ho); *Odorrana yentuensis* Tran, Orlov & Nguyen; and *Odorrana yunnanensis* Anderson (Pham et al., 2020, Frost, 2025). It is noted that the taxonomic assignment of some species has been changed. For example, *Odorrana schmackeri* was previously recorded in Vietnam by Ziegler (2002) and Nguyen et al. (2009), but recent studies suggest that this species is found only in China (Poyarkov et al. 2021, Shen et al. 2020); *Odorrana andersonii* (Boulenger, 1882) is a synonym of *Odorrana yunnanensis* Anderson, 1879 (Poyarkov et al., 2021). Therefore, further studies are required to elucidate the actual species richness of the genus *Odorrana* in Vietnam.

Acknowledgements: We are grateful to the directorates of the Forest Protection

Departments of Thai Nguyen province (formerly Bac Kan) and Lang Son provinces, as well as Ba Be National Park for their support of our field work and issuing relevant permits. We thank Phan T. Q., Ngo H. N., and Nguyen H. Q. (Ha Noi, Vietnam) for their assistance in the field. This research was supported by the National Foundation for Science and Technology Development (NAFOSTED, Grant No. 106.05-2021.19).

REFERENCES

Chen C., Mo M., Lin L., Qin K., 2024. A new species of *Odorrana* Fei, Ye & Huang, 1990 (Amphibia, Anura, Ranidae) from central Guangxi, China with a discussion of the taxonomy of *Odorrana* (*Bamburana*). *ZooKeys*, 1190: 131–152. <https://doi.org/10.3897/zookeys.1190.109886>

Felsenstein J., 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, 39: 783–791. <https://doi.org/10.1111/j.1558-5646.1985.tb00420.x>

Frost D. R., 2025. Amphibian Species of the World: an on-line reference. Version 6.2. American Museum of Natural History, New York, USA. Available from <https://amphibiansoftheworld.amnh.org/> (accessed on 10 April 2025).

Glaw F., Vences M., 2007. A field guide to the amphibians and reptiles of Madagascar. Third Edition, Frosch Verlag, Cologne, 496 pp.

Guindon S., Dufayard J. F., Lefort V., Anisimova M., Hordijk W., Gascuel O., 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. *Systematic Biology*, 59: 307–321.

Hall T. A., 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium Series, 41 (1999): 95–98.

Hoang D. T., Chernomor O., von Haeseler A., Minh B. Q., Vinh L. S., 2018. UFBoot2: Improving the Ultrafast Bootstrap Approximation. *Molecular Biology and Evolution*, 35(2): 518–522. <https://doi.org/10.1093/molbev/msx281>

Li S. Z., Chen J. J., Su H. J., Liu J., Tang X. J., Wang B., 2024. A new odorous frog species of *Odorrana* (Amphibia, Anura, Ranidae) from Guizhou Province, China. *ZooKeys*, 1192: 57–82. <https://doi.org/10.3897/zookeys.1192.114315>.

Lin S. S., Li Y. H., Su H. L., Yi H., Pan Z., Sun Y. J., Zeng Z. C., Wang J., 2022. Discovery of a new limestone karst-restricted odorous frog from northern Guangdong, China (Anura, Ranidae, *Odorrana*). *ZooKeys*, 1120: 47–66. <https://doi.org/10.3897/zookeys.1120.87067>

Luo T., Wang S., Xiao N., Wang Y., Zhou J., 2021. A new species of Odorous Frog genus *Odorrana* (Anura, Ranidae) from southern Guizhou Province, China. *Asian Herpetological Research*, 12: 381–398. <https://doi.org/10.16373/j.cnki.ahr.200122>

Minh B. Q., Nguyen M. A., von Haeseler A., 2013. Ultrafast approximation for phylogenetic bootstrap. *Molecular Biology and Evolution*, 30: 1188–1195.

Mo Y., Chen W., Wu H., Zhang W., Zhou S., 2015. A new species of *Odorrana* inhabiting complete darkness in a karst cave in Guangxi, China. *Asian Herpetological Research*, 6: 11–17. <https://doi.org/10.16373/j.cnki.ahr.140054>

Nguyen L. T., Schmidt H. A., von Haeseler A., Minh B. Q., 2015. IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, 32: 268–274.

Nguyen S. V., Ho C. T., Nguyen T. Q., 2009. Herpetofauna of Viet Nam. Edition Chimaira, Frankfurt am Main, Germany, 768 pp.

Pham C. T., Le M. D., Ngo H. T., Nguyen T. Q., 2020. New records of cascade frogs of the genus *Odorrana* (Amphibia: Anura: Ranidae) from Vietnam. Vietnam. *Academia Journal of Biology*, 42(4): 33–40.

Pham C. T., Nguyen T. Q., Bernardes M., Nguyen T. T., Ziegler T., 2016a. First records of *Bufo gargarizans* Cantor, 1842 and *Odorrana lipuensis* Mo, Chen, Wu, Zhang et Zhou, 2015 (Anura: Bufonidae) from Vietnam. *Russian Journal of Herpetology*, 23: 103–107.

Pham C. T., Nguyen T. Q., Le M. D., Bonkowski M., Ziegler T., 2016b. A new species of *Odorrana* (Amphibia: Anura: Ranidae) from Vietnam. *Zootaxa*, 4084: 421–435.

Poyarkov N. A., Nguyen T. V., Popov E. S., Geissler P., Pawangkhanant P., Neang T., Suwannapoom C., Orlov N.L., 2021. Recent progress in taxonomic studies, biogeographic analysis, and revised checklist of amphibians of Indochina. *Russian Journal of Herpetology*, 28(3A): 1–110. <https://doi.org/10.30906/1026-2296-2021-28-3A-1-110>

Rambaut A., Drummond A. J., Xie D., Baele G., Suchard M. A., 2018. Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology*, 67: 901–904. <https://doi.org/10.1093/sysbio/syy032>

Simmons J. E., 2002. Herpetological collecting and collections management. Revised edition. Society for the Study of Amphibians and Reptiles. *Herpetological Circular*, 31: 1–153

Simon C., Frati F., Beckenbach A., Crespi B., Liu H., Flook P., 1994. Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America*, 87: 651–701.

Shen H., Zhu Y., Li Z., Chen Z., Chen X., 2020. Reevaluation of the holotype of *Odorrana schmackeri* Boettger, 1892 (Amphibia: Anura: Ranidae) and characterization of one cryptic species in *O. schmackeri* sensu lato through integrative approaches. *Asian Herpetological Research*, 11: 297–311. <https://doi.org/10.16373/j.cnki.ahr.200097>

Song H. M., Zhang S., Qi S., Lyu Z. T., Zeng Z., Zhu Y., Huang M., Luan F., Shu Z., Gong Y., Liu Z., Wang Y., 2023. Redefinition of the *Odorrana versabilis* group, with a new species from China (Anura, Ranidae, *Odorrana*). *Asian Herpetological Research*, 14: 283–299. <https://doi.org/10.3724/ahr.2095-0357.2023.0019>

Song H. M., Qi S., Wang H. T., Gong Y., Liu Y., Wang Y., 2025. Definition and taxonomic revision of the karst-associated *Odorrana lipuensis* group (Anura, Ranidae), with a new species from Guangdong, China. *Zoosystematics and Evolution*, 101: 935–952. <https://doi.org/10.3897/zse.101.142746>

Tamura K., 1992. Estimation of the number of nucleotide substitutions when there are strong transition–transversion and G + C–content biases. *Molecular Biology and Evolution*, 9: 678–687.

Tamura K., Stecher G., Kumar S., 2021. MEGA 11: Molecular Evolutionary Genetics Analysis Version 11. *Molecular Biology and Evolution*, 38(7): 3022–3027. <https://doi.org/10.1093/molbev/msab120>

Thompson J. D., Gibson T. J., Plewniak F., Jeanmougin F., Higgins D. G., 1997. The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic acids research*, 25(24): 4876–4882.

Wang Y. Y., Lau M. N., Yang J. H., Chen G. L., Liu Z. Y., Pang H., Liu Y., 2015. A new species of the genus *Odorrana* (Amphibia: Ranidae) and the first record of *Odorrana bacboensis* from China. *Zootaxa*, 3999: 235–254.

Ziegler T., 2002. Die Amphibien und Reptilien eines Tieflandfeuchtwald-Schutzgebiets in Vietnam. Natur & Tier Verlag, Münster, 342 pp.