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A new species of bug-eyed tree frog, genus *Theloderma* (Amphibia: Anura: Rhacophoridae) from Vietnam

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Abstract. We describe a new species of *Theloderma* from Phia Oac–Phia Den National Park, Cao Bang Province, Vietnam based on morphological differences and molecular divergence. *Theloderma woltersi*, new species, is distinguishable from its congeners based on a combination of the following characteristics: Size small, SVL 25.1–26.2 mm in males, 30.3 mm in females; head longer than wide (HL/HW 1.15–1.18 in males and 1.09 in female); vomerine teeth absent; spines on upper eyelid absent; tibiotarsal projection absent; dorsal skin almost smooth; dermal fringes on forearm and tarsus absent; dorsal surface red-brown with some black blotches in irregular shape; and throat brown or dark brown, ventral surface of arms and thighs brown with white reticulation.

Key words. Cao Bang Province, cryptic species, *Theloderma woltersi*, new species, molecular phylogeny, taxonomy

INTRODUCTION

The amphibian family of rhacophorid tree frogs (Anura: Rhacophoridae) is a large group of arboreal frogs with around 460 species belonging to 24 genera. They can be found throughout sub-Saharan Africa; and southern Asia from Sri Lanka, Nepal and India, to Japan, the Philippines, and Sulawesi (Indonesia) (Frost, 2024). This group of frogs is adapted to an arboreal lifestyle, discernible by intercalary elements between the terminal and penultimate phalanges, expanded digit disks, and often, extensive webbing on the hands and feet (Duellman & Trueb, 1986). The genus *Theloderma* is one of the most diverse groups with 29 species, with 16 of them having been recorded from Vietnam. This genus is known for its cryptic diversity and many species were described only recently (in the last decade) such as *Theloderma annae* Nguyen, Pham, Nguyen, Ngo & Ziegler, 2016; *T. auratum* Poyarkov, Kropachev, Gogoleva & Orlov, 2018; *T. khoii* Ninh, Nguyen, Nguyen, Hoang, Siliyavong, Nguyen, Le, Le & Ziegler, 2022; *T. lacustrinum* Sivongxay, Davankham, Phimmachak, Phoumixay & Stuart, 2016; *T. nebulosum* Rowley, Le, Hoang, Dau & Cao, 2011; *T. palliatum* Rowley, Le, Hoang, Dau & Cao, 2011; *T. pyaukkya* Dever, 2017; *T. vietnamense* Poyarkov, Orlov, Moiseeva, Pawangkhanant, Ruangsuwan, Vassilieva, Galoyan, Nguyen & Gogoleva, 2015. Poyarkov et al. (2015) subdivided the genus *Theloderma* into three groups, namely the *T. asperum* group, the *T. laeve* group and the *T. leporosum* group. The *T. leporosum* group is considered the one containing the most cryptic species.

Recent studies in the border region between Vietnam and China, including provinces such as Lao Cai, Yen Bai and Ha Giang, have led to the discoveries of many new amphibian species of the family Rhacophoridae. For example, *Rhacophorus larissae* (Ostroshabov, Orlov & Nguyen, 2013) and *Gracixalus sapaensis* Matsui, Ohler, Eto & Nguyen, 2017 are both found in Lao Cai and Yen Bai provinces. Meanwhile, *Zhangixalus franki* Ninh, Nguyen, Orlov, Nguyen & Ziegler, 2020; *Z. jodiae* Nguyen, Ninh, Orlov, Nguyen & Ziegler, 2020 and *Theloderma khoii* Ninh, Nguyen, Nguyen, Hoang, Siliyavong, Nguyen, Le, Le & Ziegler, 2022 are all found in Ha Giang Province; (Ostroshabov et al., 2013, Matsui et al., 2017, Nguyen et al., 2020, Ninh et al., 2022). This demonstrates that the border region contains high biodiversity potential and more research should be conducted in this previously neglected region in terms of research.

During recent fieldwork in northeastern Vietnam, small tree frogs were discovered in Phia Oac–Phia Den National Park, Cao Bang Province, northern Vietnam. Molecular comparisons revealed them to be nested within the genus *Theloderma*. Closer morphological examinations showed that the individuals from Cao Bang are clearly distinguished from other known members of *Theloderma* by a combination

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Table 1. Samples used in this study along with their associated vouchers, localities, and Genbank accession numbers. Bold text denotes new samples in this study.

No	Species	Voucher	Locality	Genbank accession no.
1.	*Theloderma bicolor*	VNMN010811	Lai Chau, Viet Nam	LC641699
2.	*T. bicolor*	VNMN010821	Lai Chau, Viet Nam	LC641670
3.	*T. khoii*	VNMN012758	Ha Giang, Viet Nam	LC641701
4.	*T. khoii*	VNMN012757	Ha Giang, Viet Nam	LC641702
5.	*T. corticale*	corticale-2	Ninh Binh, Vietnam	KT461886
6.	*T. corticale*	corticale-1	Ninh Binh, Vietnam	KT461885
7.	*T. corticale*	AMNH A161499	Vinh Phuc, Viet Nam	DQ283050
8.	*T. corticale*	ZMMU NAP-06328	Vinh Phuc, Viet Nam	MG917764
9.	*T. rhododiscus*	SCUM 061102L	Jinxiu, Guangxi, China	EU215530
10.	*T. rhododiscus*	YU000309	Huanjiang, Guangxi, China	OL843959
11.	*T. rhododiscus*	YU000318	Longlin, Guangxi, China	OL843960
12.	*T. rhododiscus*	YU000319	Longlin, Guangxi, China	OL843961
13.	*T. hekouense*	YU000398	Hekou, Yunnan, China	OL843963
14.	*T. hekouense*	YU000412	Hekou, Yunnan, China	OL843964
15.	*T. hekouense*	YU000413	Hekou, Yunnan, China	OL843965
16.	*T. hekouense*	YU000495	Hekou, Yunnan, China	OL843966
17.	***Theloderma woltersi*, new species**	**IEBR A.5244**	**Cao Bang, Vietnam**	**PP756489**
18.	***Theloderma woltersi*, new species**	**IEBR A.5245**	**Cao Bang, Vietnam**	**PP756490**
19.	***Theloderma woltersi*, new species**	**IEBR A.5246**	**Cao Bang, Vietnam**	**PP756491**
20.	*T. palliatum*	ZMMU NAP-01846	Lam Dong, Vietnam	KT461901
21.	*T. palliatum*	ZMMU NAP-02516	Lam Dong, Vietnam	KT461903
22.	*T. auratum*	ZMMU A-5832	Kon Tum, Vietnam	MG917771
23.	*T. auratum*	ZMMU NAP-06402-2	Kon Tum, Vietnam	MG917772
24.	*T. leporosum*	LJT W46	Malaysia	KC465841
25.	*T. leporosum*	Tlep1	Selangor, Malaysia	KT461922
26.	*T. lateriticum*	IEBR 3745	Lao Cai, Vietnam	LC641703
27.	***T. lateriticum***	**IEBR 3748**	**Hoa Binh, Vietnam**	**PP756487**
28.	***T. lateriticum***	**IEBR 4219**	**Cao Bang, Vietnam**	**PP756488**
29.	*T. lacustrinum*	NCSM84682	Laos	KX095245
30.	*T. lacustrinum*	NCSM84683	Laos	KX095246
31.	*T. truongsonense*	ZMMU NAP-07142	Gia Lai, Vietnam	MG917762
32.	*T. truongsonense*	ZMMU NAP-07143	Gia Lai, Vietnam	MG917763
33.	*Rhacophorus kio*	KUHE:55165	Thanh Hoa, Vietnam	AB781695
34.	*R. kio*	SCUM 37941C	Yunnan, China	EU215532
35.	*R. calcaneus*	KIZ528	Lam Dong, Vietnam	JX219450
36.	*R. calcaneus*	KIZ746	Lam Dong, Vietnam	JX219451

of morphological features, reflected as well by a distinct phylogenetic position. Thus, due to distinct morphological and molecular differences, we herein describe the newly discovered *Theloderma* population from Cao Bang as a new species.

MATERIAL AND METHODS

Sampling. Field surveys were conducted in June 2019 by Tao Thien Nguyen, Manh Van Le, and Nikolai Orlov in Phia Oac–Phia Den National Park, Cao Bang Province, northern Vietnam. Specimens were collected between 1900 and 2300 hours. After taking photographs, they were anaesthetised and euthanised in a closed vessel with a piece of cotton wool containing ethyl acetate, fixed in 80% ethanol for 4–6 hours, then transferred to 70% ethanol for permanent storage. Tissue samples were preserved separately in 95% ethanol. Preserved specimens were deposited in the scientific collection of the Institute of Genome Research, Hanoi, Vietnam. Other specimens referred to in this paper are deposited at the Institute of Ecology and Biological Resources (IEBR), Hanoi, Vietnam.

Molecular data and phylogenetic analyses. We used the protocols of Kuraishi et al. (2013), modified by Nguyen et al. (2015), for DNA extraction, amplification, and sequencing. Fragments of 16S rRNA of mitochondrial was amplified using the primers following Kuraishi et al. (2013). *Rhacophorus calcaneus* Smith, 1924 and *R. kio* Ohler & Delorme, 2006 were selected as outgroups (Table 1).

Chromas Pro software (Technelysium Pty Ltd., Tewantin, Australia) was used to edit the sequences, which were aligned using MAFFT version 7 (Katoh & Standley, 2013) with default settings. We then checked the initial alignments by eye and adjusted them slightly. Phylogenetic trees were constructed by using maximum likelihood (ML) and Bayesian inference (BI). Before ML and Bayesian analyses, we chose the optimum substitution models for entire sequences using Kakusan 4 (Tanabe, 2011) based on the Akaike information criterion (AIC). The best model selected for ML was the general time-reversible model (GTR: Tavaré, 1986) with a gamma shape parameter (G: 0.307 in ML and 0.35 in BI). The BI summarised two independent runs of four Markov Chains for 10,000,000 generations. A tree was sampled every 100 generations and a consensus topology was calculated for 70,000 trees after discarding the first 30,001 trees (burn-in = 3,000,000). We checked parameter estimates and convergence using Tracer version 1.5 (Rambaut & Drummond, 2009). The strength of nodal support in the ML tree was analyzed using non-parametric bootstrapping (MLBS) with 1000 replicates. We regarded tree nodes in the ML tree with bootstrap values of 70% or greater as sufficiently resolved (Huelsenbeck & Hillis, 1993) and nodes with a BPP of 0.95 or greater as significant in the BI analysis (Leaché & Reeder, 2002). Pairwise comparisons of uncorrected sequence divergences (p-distance) were calculated for 16S rRNA fragments only between species of the genus *Theloderma* using MEGA 7 (Kumar et al., 2016).

Morphological characters. Measurements were taken with a digital calliper to the nearest 0.1 mm.

Abbreviations are as follows:
SVL: snout – vent length;
HL: head length (from the back of mandible to the tip of snout);
HW: maximum head width (across angle of jaws);
SNL: snout length (from anterior corner of eye to the tip of snout);
NS: distance from nostril to the tip of snout;
EN: distance from anterior corner of the eye to the nostril;
IN: internarial distance;
IOD: interorbital distance;
ED: eye diameter (the distance between the two corners of the eyes);
UEW: maximum width of upper eyelid;
DAE: distance between anterior corner of eyes;
DPE: distance between posterior corners of eyes;
MAE: distance between angle of jaws and anterior corner of the eye;
MPE: distance between angle of jaws and posterior corner of the eye;
MN: distance from the back of mandible to the nostril;
TYD: tympanum diameter (Maximum distance of the tympanic rim);
TYE: distance from anterior margin of tympanum to posterior corner of the eye;
FLL: forelimb length (from axilla to elbow);
HAL: hand length (from elbow to the tip of third finger);
FL3: third finger length (from the base to the fingertips 3);
fd3: Width of discs of fingers 3;
FeL: Femur length (from vent to knee);
TbL: tibia length (from knee to tarsus);
TbW: maximum tibia width;
FoL: foot length (from tarsus to the tip of fourth toe);
TL4: fourth toe length (from the inner metatarsal to the tip of the toe 4);
td4: width of discs of toes IV.

Terminology for describing eye colouration in life and webbing formula followed those of Glaw & Vences (1997, 2007). Sex was determined by the presence of nuptial pads and gonadal inspection.

RESULTS

Phylogenetic analyses. Aligned, combined sequences of 16S rRNA yielded a total of 808 bp. Of 808 nucleotide sites, 286 were variable and 271 were parsimony informative within the ingroup. The ML and Bayesian analyses produced topologies with -lnL = 4399,8431 and 4457,056 respectively.

Phylogenetic analyses employing ML and BI methods yielded slightly different topologies only among referenced species. Only the BI tree is presented in Fig. 1. The unidentified species of *Theloderma* from Cao Bang was placed in the clade containing *Theloderma rhododiscus* and *T. hekouense* with strong support (MLBS = 100%, BPP = 1.00) (Fig. 1).

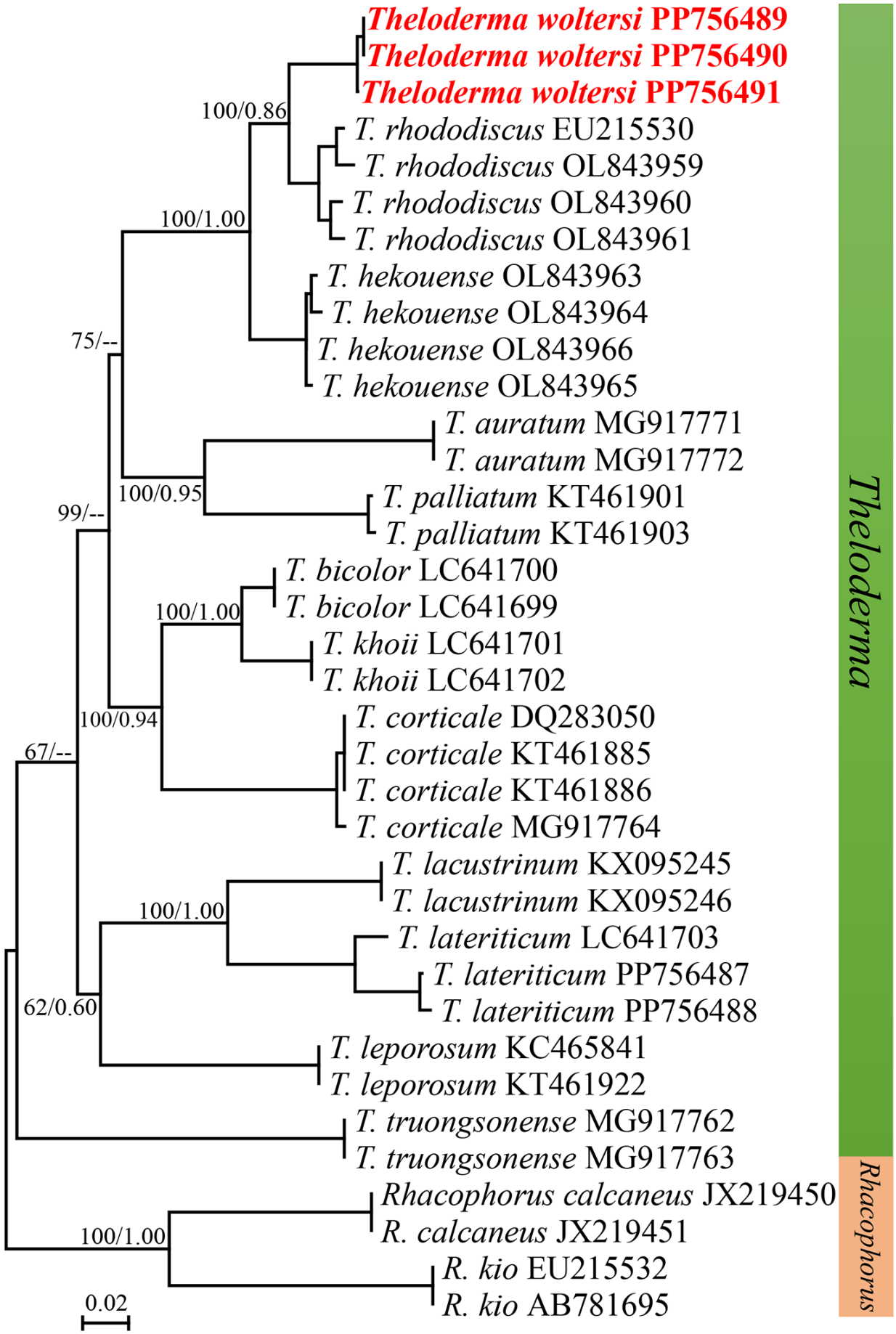

Fig. 1. BI tree from 808 bp sequence of mitochondrial 16S rRNA gene of *Theloderma* and outgroup species. Numbers above and below branches are Bayesian posterior probabilities (values ≥ 0.95 shown) and ML bootstrap values (values ≥70 shown), respectively; for GenBank accession numbers, see Table 1.

Fig. 2. *Theloderma woltersi*, new species, male holotype (IEBR.A.5246) in life.

The interspecific uncorrected genetic p-distances between the unnamed *Theloderma* species from Cao Bang and all congeners analysed at the fragment of 16S rRNA gene examined varied from approximately 3.90% (compared with *T. rhododiscus*) to 13.81% (compared with *T. truongsonense*) (Table 2).

The newly collected *Theloderma* was closely related to *T. rhododicus* from Guangxi, China (Jinxiu, Huanjiang, and Longlin) and *T. hekouense* from Yunnan, China (Hekou). The genetic distance between the newly collected specimens to *T. rhododiscus* and *T. hekouense* ranged from 3.90–5.25, with their monophyly being strongly supported (BPP = 1.00, BS = 1.00%).

Such a degree of pairwise divergence in the 16S rRNA gene in frogs has been interpreted previously as indicative of differentiation at the species level (Hebert et al., 2003). Furthermore, the newly discovered *Theloderma* population from northern Vietnam is also clearly separated morphologically from all congeners. Thus, we conclude it represents a distinct species in the genus *Theloderma*.

TAXONOMY

Family Rhacophoridae Hoffman, 1932

Genus *Theloderma* Tschudi, 1838

Theloderma woltersi, new species

(Figs. 2, 3)

Holotype. IEBR.A.5246 (Field number CB.010828), adult male, collected by T. T. Nguyen et al., in June 2019, in the forest near Phia Oac–Phia Den National Park, at an elevation of 1,900 m), Cao Bang Province, northern Vietnam.

Paratypes. Two adult males IEBR.A.5247, IEBR.A.5245 (CB.010824, CB.010827) and one adult female IEBR.A.5244 (CB.010826) specimen were collected in June 2019 by the same team and with the same data as the holotype.

Diagnosis. Morphologically, the new species from Cao Bang Province can be assigned to the genus *Theloderma* by a combination of the following characteristics: Small in size (SVL 25.1–26.2 mm in males, 30.3 mm in female), distinct

Table 2. Mean uncorrected ("p") distance (%) among 808 bp fragments of 16S rRNA from species of the genus *Theloderma*

Theloderma woltersi, new species	0.00–0.26												
T. auratum	12.17–12.28	0.00											
T. bicolor	9.79–10.37	10.28–10.58	0.00										
T. corticale	11.40–11.73	11.32–11.77	8.37–8.58	0.00–0.63									
T. hekouense	4.19–5.25	8.76–10.94	6.90–9.83	8.96–11.14	0.16–0.66								
T. khoii	11.11–11.20	11.35–11.44	3.66–3.68	9.17–9.24	7.05–9.84	0.00							
T. lacustrinum	13.37–13.58	14.67	11.50–11.87	13.54–13.56	10.58–13.73	12.44–12.53	0.00						
T. lateriticum	13.46–14.21	14.00–15.06	12.30–13.39	12.73–13.92	10.29–14.10	13.40–13.58	8.74–9.82	0.52–3.92					
T. leporosum	12.48–12.57	11.97–12.27	10.63–10.96	11.13–11.18	9.11–11.67	10.88–10.92	11.88–11.98	11.93–13.02	0.00				
T. palliatum	11.63–11.87	10.39–10.64	10.91–11.23	11.27–15.53	8.21–10.49	11.80–11.93	13.22–13.46	13.31–14.27	11.83–11.93	0.39			
T. rhododiscus	3.90–4.44	11.71–12.76	10.74–11.50	10.53–11.39	3.96–4.95	10.98–11.38	12.92–13.45	13.15–13.68	11.77–12.50	11.42–12.16	0.91–2.08		
T. truongsonense	13.74–13.81	13.84	12.80	14.63–14.84	10.47–13.16	12.78–12.88	14.78	14.93–17.32	14.61–14.69	14.38–14.65	13.91–14.70		
R. calcaneus	13.64–13.91	14.67	13.89–14.21	13.92–14.21	10.73–13.37	14.36–14.47	16.27	16.34–17.32	15.44–15.51	14.68–14.92	12.94–13.70	15.55	
R. kio	14.95–15.24	15.34	15.73–16.39	16.58–16.95	11.90–14.55	15.54–15.67	15.89	16.86–17.59	15.34–15.54	15.07–15.45	14.14–15.04	14.41	12.11

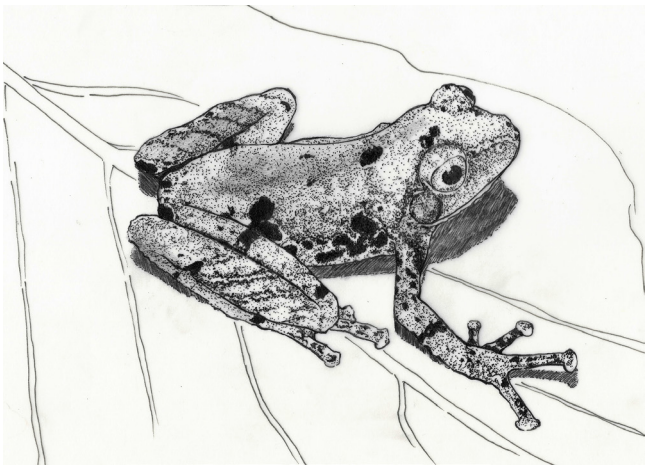

Fig. 3. Drawing of *Theloderma woltersi*, new species, male holotype (IEBR.A.5246).

tympanum, round canthus rostralis, bony ridges from canthus rostralis to occiput lacking, and skin of head not co-ossified to the skull, tip of finger dilated into disc (see Liem, 1970; McLeod & Ahmad, 2007; Rowley et al., 2011; Hou et al., 2017). However, because morphological synapomorphies are lacking for the genus *Theloderma*, and thus its monophyly is not certain (Bain et al., 2009; Li et al., 2009; Rowley et al., 2011) we additionally used molecular evidence to provide independent support for the species' distinctiveness and its phylogenetic placement within *Theloderma*.

The new species is distinguished from its congeners and other larger rhacophorid species from Vietnam, south China, Northeast India, and mainland Southeast Asia by a combination of the following characters: 1) Size small (SVL 25.1–26.2 mm in males, 30.3 mm in female); 2) head longer than wide (HL/HW 1.15–1.18 in males and 1.09 in female); 3) vomerine teeth absent; 4) snout pointed and truncated (SL/SVL 0.15–0.18 in male; 0.14 in female); 5) eye large, without spines on upper eyelid; tympanum distinct, with distinct tympanic annulus; 6) tibiotarsal articulation reaches beyond tip of snout; 7) dorsal skin slightly rough with large irregular gland ridges and warts, ventral surface granular; 8) webbing between fingers weak (I1½–1½II¾–1¾III1¾–1¾IV), webbing between toes moderate (I½–1½II1¼–1¾III½–1¾IV¾–¾V); tips of all digits dilated but all considerably smaller than tympanum; 9) dorsal surface brown with dark spots; and 10) lateral and ventral body cream with blotches; and 11) large nuptial pads and an inner vocal sac in males.

Description of holotype. Adult male, small-sized (SVL 25.1 mm), body distinctly flattened, dorsoventrally compressed; head longer than wide (HL/HW 1.2); snout pointed and truncated, its length about 0.16 body length; canthus rostralis oval, very oblique, slightly concave loreal region; interorbital distance wider than internarial distance and upper eyelid (IOD/IN 1.2; IOD/UEW 1.1); distance between anterior corner of eyes about 0.6 distance between posterior corner of eyes; nostril oval, laterally directed, inside the rather enlarged tubercle on the tip of snout, nostrils closer to tip of the snout than to eyes (NS/EN 0.6); pupil circular; tympanum nearly

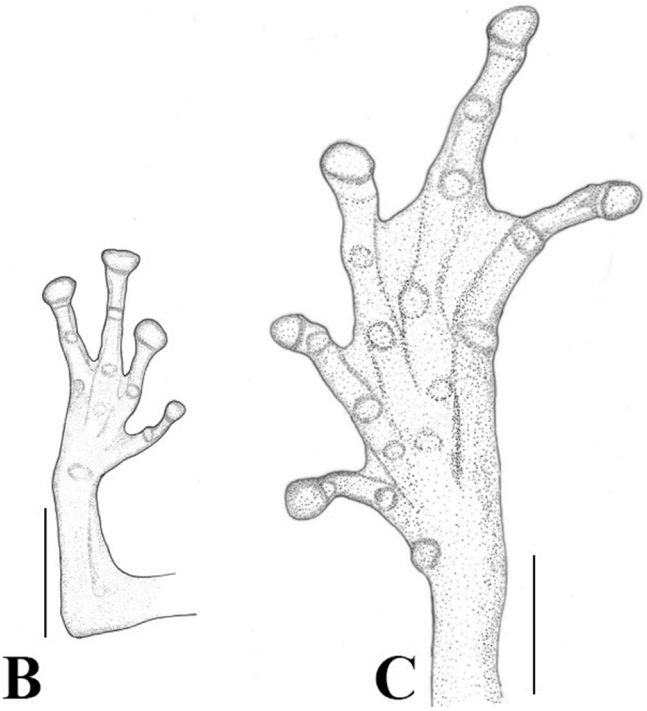

Fig 4. Drawing of undersides of right hand and left foot of *Theloderma woltersi*, new species, male holotype (IEBR.A.5246).

two times the width of third finger disk (TYD/fd3 2.5), separated from eye by 0.3 of tympanum length (TYE/TYD 0.3); pineal ocellus absent; spinules on upper eyelid absent; supratympanic fold distinct but intermittent, extending from behind the eye to beyond level of the axilla, composed of large irregular gland ridges closely arranged; vomerine teeth absent; tongue large, almost covering half of mouth, heart-shaped, dorsal surface smooth, bifid and free posteriorly; vocal sacs indistinct.

Forelimbs moderately strong and long, (FLL 4.9 mm, HAL 12.7 mm); relative length of fingers: I < II < IV < III; tips of fingers dilated into large, rounded and flattened disks, with grooves separating dorsum of disks from venter; disc of finger III approximately half of tympanum diameter (fd3/TYD 0.4); subarticular tubercles large and distinct, with indistinct supernumerary tubercles; subarticular tubercle formula: 1, 1, 2, 2; nuptial pad on lateral side of thumb well developed; outer side of fourth finger fringed and distinctly serrated; webbing between fingers weakly developed, about 50% between base and proximal subarticular tubercles, webbing formula I1½–1½II¾–1¾III1¾–1¾IV (Fig. 4)

Hindlimbs strong and long, tibia length about five times greater than tibia width (TbL 14.0 mm, TbW 2.8 mm); tibia length about five times greater than tibia width (TbL/TbW 5.0), longer than thigh length and shorter than foot length (TbL/FeL 1.1; TbL/FoL 0.8), tibiotarsal articulation reaching the posterior edge of snout when hindlimbs adpressed forward; relative length of toes I < II < V < III < IV; toes with rounded disks, tips of toes dilated into flattened disks with grooves that separate dorsum of disks from venter, smaller than the ones on fingers; webbing formula I½–1½II1¼–1¾III½–1¾IV¾–¾V (Fig. 4); large

Table 3. Measurements (in mm) and proportions of the type series of *Theloderma woltersi*, new species, (H = holotype, P = paratype, other abbreviations defined in text).

Specimen number	**IEBR.A.5246**	**IEBR.A.5245**	**IEBR.A.5247**	**IEBR.A.5244**
Sex	**Male**	**Male**	**Male**	**Female**
	Holotype	**Paratype**	**Paratype**	**Paratype**
Locality	**Cao Bang**	**Cao Bang**	**Cao Bang**	**Cao Bang**
SVL	25.1	26.2	25.5	30.3
HL	9.9	9.6	10.3	11.3
HW	8.6	8.3	8.7	10.4
SNL	4.0	4.0	4.5	4.4
NS	1.4	1.2	1.7	1.4
EN	2.3	2.4	2.7	2.7
IN	2.5	2.7	2.7	2.8
IOD	3.0	3.2	3.2	3.3
ED	3.3	3.2	3.1	3.5
UEW	2.7	2.3	2.5	3.0
DAE	5.3	5.2	5.4	6.1
DPE	8.0	7.9	8.1	9.0
MAE	6.6	6.5	6.7	8.3
MPE	4.1	4.5	4.0	5.3
MN	9.0	8.7	9.4	10.3
TYD	2.5	2.4	2.6	3.0
TYE	0.8	1.1	1.0	0.8
FLL	4.9	5.2	5.5	6.4
HAL	12.7	12.9	13.0	9.9
FL3	5.6	5.4	4.6	5.1
fd3	1.0	1.1	1.3	1.4
FeL	12.6	12.9	11.5	16.0
TbL	14.0	14.4	14.4	17.3
TbW	2.8	2.6	3.1	3.0
FoL	18.4	18.0	18.4	18.8
TL4	11.8	11.2	11.3	13.8
td4	0.8	1.2	1.2	1.2
HL/HW	1.2	1.2	1.2	1.1
SNL /SVL	0.2	0.2	0.2	0.1
IOD/IN	1.2	1.2	1.2	1.2
IOD/UEW	1.1	1.4	1.3	1.1
DAE/DPE	0.7	0.7	0.7	0.7
NS/EN	0.6	0.5	0.6	0.5
TYE/TYD	0.3	0.5	0.4	0.3
TYD/fd3	2.5	2.2	2.0	2.1
TbL/TbW	5.0	5.5	4.6	5.8
TbL/FeL	1.1	1.1	1.3	1.1
TbL/FoL	0.8	0.8	0.8	0.9

Fig. 5. Habitat of *Theloderma woltersi*, new species, in Phia Oac–Phia Den National Park, Cao Bang Province, Northeastern Vietnam.

subarticular tubercles roundish: 1, 1, 2, 3, 2; large inner metatarsal tubercle oval and raised, without outer metatarsal tubercle; with small warts on the inner aspect of metatarsal area; the outer side of the fifth toe fringed, distinctly serrated.

Skin texture in life. Dorsal surface of head, dorsum, arms and legs generally smooth, but with some very small tubercles; outer side of limbs and flank with granules, throat and chest smooth, belly and ventral side of thighs slightly granular, supratympanic and dorsolateral folds absent.

Colouration in life. Background of dorsal surface reddish-brown with two to four small black blotches; flank displays well-defined cream and dark grey pattern; dorsal surface of the forelimbs with a black bar in the middle of the arm, fingertips brown, and the hindlimbs have a black bar at the middle of the thigh and a dark bar in the middle of the tibia; dorsal surface of hindlimbs light brown with black or dark grey blotches; belly and ventral surface of limbs cream with larger dark blotches forming a network; chin and throat dark brown with small white spots; tips of toes and fingers red-orange; loreal area dark grey without spots; supratympanic line reddish; iris red-orange; pupils black.

Colouration in preservative. The red-brown, red-orange, and reddish colour pattern in life fades into grey or greyish in preserved state.

Sexual dimorphism and variation. Males are smaller than females and can be further distinguished from females by the presence of nuptial pads.

Etymology. We dedicate the species name to the late Jürgen Wolters, founding member of Stiftung Artenschutz, which supports current conservation-based mossy frog research in Vietnam. Furthermore, Stiftung Artenschutz has been dedicated to supporting amphibian research through its specialised amphibian program for over 15 years.

Ecological notes. *Theloderma woltersi*, new species, was found in a water tank near a ranger station at an elevation of 1,900 m a.s.l. (Fig.5).

Distribution and conservation status. *Theloderma woltersi*, new species, is currently known only from the type locality in Phia Oac–Phia Den National Park, Cao Bang Province, northern Vietnam (Fig. 6).

Comparisons. We compare the new species with all species in the genus *Theloderma* in Vietnam and bordering countries.

Theloderma woltersi, new species, can be distinguished from *T. bicolor*, *T. corticale*, *T. gordoni*, *T. ryabovi*, and *T. truongsonense* by its small size (SVL 25.1–26.2 in males and 30.3 in female of *Theloderma woltersi*, new species, vs. SVL> 42–46.5 in males in *T. bicolor* (Bourret, 1937); vs. 61.3–69.7 in males and 58–69 in females in *T. corticale* (Boulenger, 1903; Luu et al., 2013; Hecht et al., 2013; Chen et al., 2018); vs. 57.5–70 in males and 71.7 in females in *T. gordoni* (Taylor, 1962, Qi et al., 2018,), vs. 52.2–59.4 in males in *T. khoii* (Ninh et al., 2022); vs. 43.84 in the male *T. ryabovi* (Orlov et al., 2006).

Theloderma woltersi, new species, can be distinguished from other species with similar sizes based on the following combination of morphological characteristics (see also Table 4):

Theloderma woltersi differs from *T. albopunctatum* by having a red-brown dorsum with some black blotches, ventral surface cream with larger dark blotches forming reticulation, iris red-orange vs. dorsum brown with some white markings, ventral surface greyish with white blotches, iris red-brown in *T. albopunctatum* (Liu & Hu, 1962); from *T. annae* by having a red-brown dorsum with some black blotches, belly and ventral surface cream with larger dark blotches forming reticulation, iris red-orange vs. dorsal surface greyish green, with some mossy green, belly immaculate white, iris greyish green in *T. annae* (Nguyen et al., 2016); from *T. asperum* by having a red-brown dorsum with some black blotches, belly and ventral surface cream with larger dark blotches forming reticulation, iris red-orange vs. dorsal surface of head and body bluish grey with a small brown line between eyes while the posterior part has a large chocolate area, venter blueish grey white and marbled black, brownish on the underside of arms and limbs, iris reddish brown in *T. asperum* (Neang & Holden, 2008, Hecht et al., 2013, Luu et al., 2014,); from *T. auratum* by having a red-brown dorsum with some black blotches, belly and ventral surface cream with larger dark blotches forming reticulation, iris red-orange vs. dorsal surface golden-yellow with numerous tiny flat golden-orange tubercles, ventral surface greyish-blue with indistinct brown confluent blotches, getting smaller and denser anteriorly, forming a dense brownish pattern on throat, iris golden above and black below in *T. auratum* (Poyarkov et al., 2018); from *T. gordoni* by having a red-brown dorsum with some black blotches, belly and ventral surface cream with larger dark blotches forming reticulation, iris red-orange vs. dark brown or coffee dorsum, ventral surface dark blue with numerous irregular greyish white patterns and speckles, iris pale bluish-white with irregular black patterns in *T. gordoni* (Qi et al., 2018); from *T. laeve* by having head

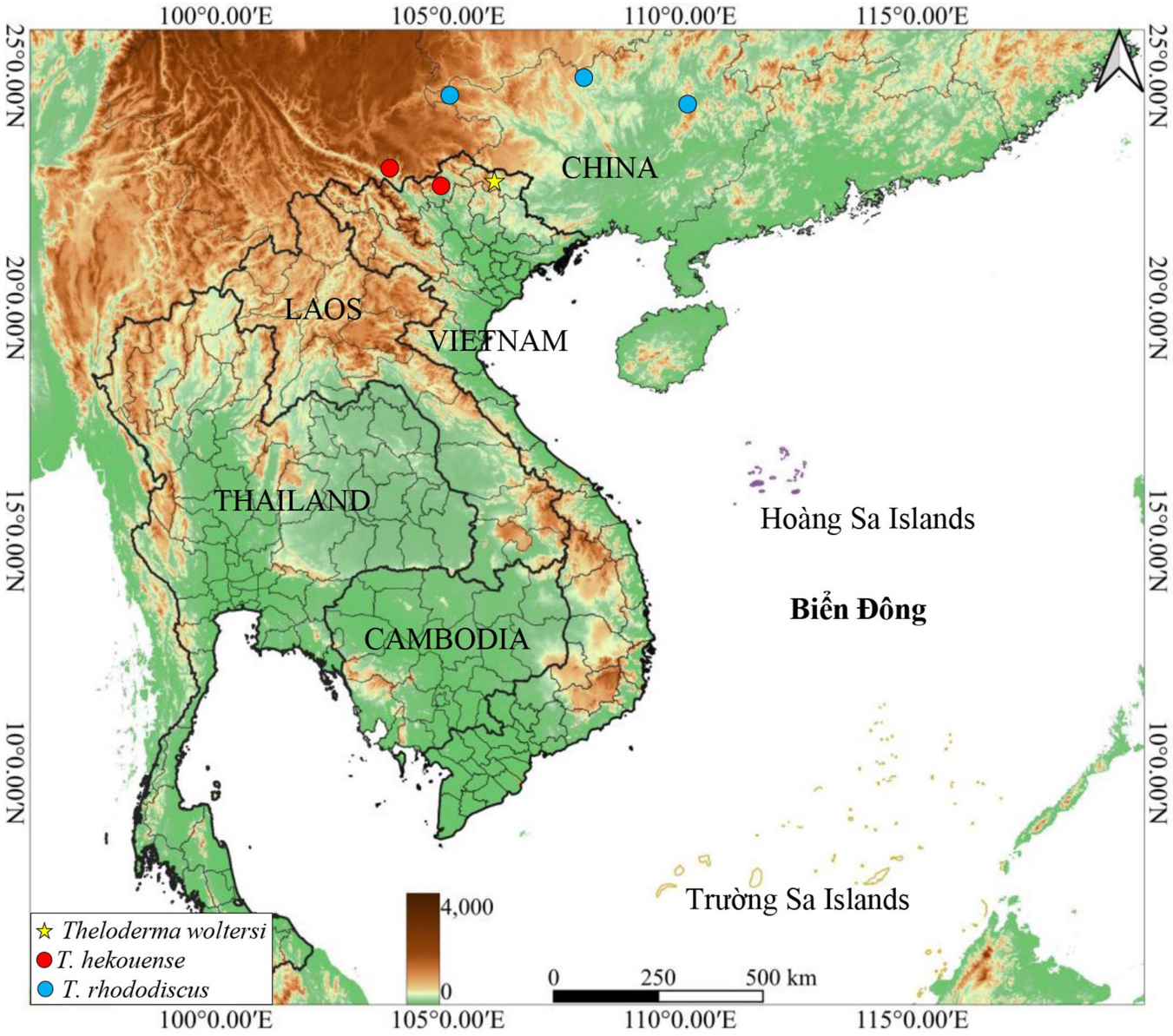

Fig. 6. Map showing the distribution of *Theloderma woltersi*, new species, *T. hekouense*, and *T. rhododiscus*.

length longer than width, a red-brown dorsum with some black blotches, belly and ventral surface cream with larger dark blotches forming reticulation vs. head length as long as head width, a beige dorsum, ventral pure white in *T. laeve* (Smith, 1924); from *T. nebulosum* by having a red-brown dorsum with some black blotches, belly and ventral surface cream with larger dark blotches forming reticulation, iris red-orange vs. brown dorsum with indistinct darker brown longitudinal markings running along the midline from the snout, ventral surface of body brownish black with pale bluish white marbling on chest, faint white speckling on throat, iris pale gold above and reddish brown below in *T. nebulosum* (Rowley et al., 2011); from *T. palliatum* by having fingers webbed and a red-brown dorsum with some black blotches, ventral surface cream with larger dark blotches forming reticulation, iris red-orange vs. finger webbing absent, a pale brown dorsum with dark brown markings, ventral surface warm dark brown, iris pale gold in upper third, and dark reddish brown in lower two-thirds in *T. palliatum* (Rowley et al., 2011; from *T. petilum* by having fingers webbed, a red-brown dorsum with some black blotches, belly and ventral surface cream with larger dark blotches forming reticulation vs. finger webbing absent, a light brown dorsum with dark brown reticulations and scattered black spotting, ventral creamy white in *T. petilum* (Nguyen et al., 2014); from *T. rhododiscus* by having a mostly smooth red-brown dorsum with some black blotches, cream ventral with black blotches forming reticulation vs. dorsum tea-brown with numerous minute whitish granules arranged in a reticulation on the back, while the ventral surface has a dark grey or black background with white spots in *T. rhododiscus* (Liu et al., 1962, Du et al., 2022) (Fig. 7); from *T. truongsonense* by having fingers webbed, a red-brown dorsum with some black blotches, belly and ventral surface cream with larger dark blotches forming reticulation, iris red-orange vs. finger webbing absent, yellow-goldish dorsum separated from dark-grey ventral surface by a black stripe passing from the snout across eye and tympanum to anal region, iris golden yellow above and black below in *T. truongsonense* (Orlov & Ho, 2005); from *T. vietnamense* by having a smooth reddish

Fig. 7. Dorsal and ventral views of *Theloderma woltersi*, new species, *T. hekouense*, and *T. rhododiscus* (Du et al., 2022). Black bars scale to 1 cm.

brown dorsum with some tubercles and black blotches, belly and ventral surface cream with larger dark blotches forming reticulation, iris red-orange vs. surface rough with large ridges and warts, diurnally dark brownish-grey with distinct dark blackish-brown blotches and warm brown markings, centre dorsum large blackish-brown blotch forming a distinct dark-brown chevron of an inverted U-shape, ventral surfaces dark blackish-brown with a purple tint being especially prominent in the throat and chin area, iris golden-brownish in *T. vietnamense* (Poyarkov et al., 2015).

Morphologically, the new species is very similar to *T. hekouense* and *T. rhododiscus*, but it can be distinguished from the aforementioned two species by combined characters: It differs from *T. hekouense* in the red-brown dorsum, mostly smooth in *Theloderma woltersi*, new species, vs. dorsum tea-brown, very rough with prominent irregular ridges, conical tubercles, and dense white small warts on top of head, upper eyelids, and upper side of limbs in *T. hekouense* (Du et al., 2022) (Fig. 7).

The new species differs from *T. rhododiscus* by a mostly smooth red-brown dorsum with some black blotches, and cream venter with black blotches forming a reticulation vs. tea-brown dorsum with numerous minute whitish granules arranged in a reticulation, and the ventral surface dark with white spots in *T. rhododiscus*.

DISCUSSION

Five *Theloderma* species have been described as new to science from Vietnam in the past 10 years, namely: *T. annae*, *T. auratum*, *T. hekouense*, *T. khoii*, and *T. vietnamense*. *T. hekouense* was originally described from China and later recorded from Vietnam, while *T. annae* and *T. khoii* were

Table 4. Morphological comparison of members of *Theloderma* with small size (SVL < 35 mm). "?" means unknown.

	Species	Iris colour	Finger webbing	Colour of discs	Dorsal colour	Ventral colour	Vomerine teeth	Vocal sac	Dorsal skin	Metacarpal, metatarsal, and subarticular tubercles
1	*Theloderma woltersi,* new species	red-orange	present	both dorsal and ventral surfaces brown	surface reddish-brown	cream with larger dark blotches forming a network	absent	absent	smooth with some tubercles	faint white
2	*T. albopunctatum*	red-brown	present	both dorsal and ventral surfaces brown	brown with white markings	dark olive with white stripes	absent	present	smooth with small asperities	greyish white
3	*T. annae*	greyish green	absent	both dorsal and ventral surfaces greyish-white	greyish green	white	absent	absent	smooth	grey
4	*T. asperum*	reddish brown	absent	both dorsal and ventral surfaces brown	bluish grey with brown markings	marbled black and bluish-grey/white	absent	present	rough with large asperities	?
5	*T. auratum*	golden above and black below	absent	dorsal surface dark brown and ventral surface grey	golden-yellow	greyish-blue with brown blotches	absent	absent	smooth	grey
6	*T. baibungense*	red-brown	absent	dorsal surface black brown and ventral surface grey	brown with white markings	black with white stripes	absent	present	smooth with small asperities	white
7	*T. hekouensis*	red-brown	absent	both dorsal and ventral surfaces orange red	tea-brown with no white markings	brownish-black with white marbled network	absent	absent	coarsely rough with large asperities	red
8	*T. lacustrinum*	uniformly bronze	absent	dorsal and ventral surfaces bronze	light brown	uniformly grey	absent	?	smooth with small asperities	grey

	Species	Iris colour	Finger webbing	Colour of discs	Dorsal colour	Ventral colour	Vomerine teeth	Vocal sac	Dorsal skin	Metacarpal, metatarsal, and subarticular tubercles
9	*T. lateriticum*	deep brick-red	absent	both dorsal and ventral surfaces grey	Brick-red	grey-brown with white spots	absent	absent	granular with small bumps	grey brown
10	*T. laeve*	grey above and dark brown below	absent	both dorsal and ventral surfaces grey	beige with thin light middorsal stripe	uniformly violet-grey	absent	absent	smooth	grey
11	*T. licin*	red	present	dorsal surface black brown	pale whitish brown to light brown	white with brown reticulation	absent	present	nearly smooth with fine asperities	?
12	*T. nebulosum*	pale gold above and reddish brown below	absent	both dorsal and ventral surfaces brown	brown with dark patterning	dark brownish black with pale blue/white marbling	absent	?	nearly smooth with very sparsely distributed minute asperities	brown
13	*T. palliatum*	pale gold above and dark red below	absent	both dorsal and ventral surface brown to greyish brown	pale to medium brown with dark brown blotches	warm dark brown with pale bluish white marbling	absent	absent	weakly rugose with sparsely scattered minute asperities	faint white
14	*T. petilum*	reddish brown above and grey below	absent	dorsal surface lavender and ventral surface creamy-white	light brown with dark brown reticulations	creamy white	present	?	nearly smooth with white small asperities	cream-white
15	*T. pyaukkya*	uniformly red	absent	dorsally red and ventrally brown	brown with white markings	brown with cream marbling	absent	present	rough with fine asperities	greyish white
16	*T. rhododiscus*	uniformly red-brown	absent	both dorsal and ventral surface red	tea brown with black blotches	brownish black with grey white network	absent	absent	rough with large asperities	white
17	*T. stellatum*	dark gold with black	present	dorsal surface reddish and ventral surface grey	brown with white markings	cream with purplish-brown flecks or spots	absent	absent	rough with small or large asperites	flesh-white

	Species	Iris colour	Finger webbing	Colour of discs	Dorsal colour	Ventral colour	Vomerine teeth	Vocal sac	Dorsal skin	Metacarpal, metatarsal, and subarticular tubercles
18	*T. truongsonense*	golden yellow above and black below	absent	dorsal surface beige to black brown and ventral surface	yellow-goldish with dark brown	dark-grey with black speckles	absent	?	smooth with small asperities	grey
19	*T. vietnamense*	golden-brownish	present	dorsally reddish and ventrally grey	brown with white markings	dark-brown to blackish with slight whitish to bluish reticulatioins	absent	present	rough with large ridges and warts	whitish to bluish

originally described from Vietnam but recorded from China later. The geographic distance between *Theloderma woltersi*, new species, and *T. hekouense* is not far (it is approximately 100 km from the type locality of *Theloderma woltersi*, Ha Giang, to the type locality of *T. hekouense*, Hekou). Northern Vietnam represents an area of high *Theloderma* species diversity, with nine recorded species so far. The discovery of another new species of *Theloderma* in Northern Vietnam is unexpected and suggests that the current species richness of the genus remains underestimated. Our record brings the total number of amphibians known in Vietnam to 287 and the total number of Rhacophoridae species known in the world to 458 (Frost, 2024). This further underlines the role of primeval forests in the higher mountains of Phia Oac–Phia Den National Park as well as other higher mountains in Vietnam as a key territory for the preservation of herpetofauna diversity in Vietnam. More studies using an integrative approach, i.e., combining morphological and molecular data, will certainly help to better reveal the extent of species richness of *Theloderma*, particularly in the poorly studied regions of northern Vietnam. Improved conservation and more conservation-based mossy frog research in the country is also one of the goals of the current EAZA (European Association of Zoos and Aquaria) conservation campaign 'Vietnamazing' (Ziegler et al., 2024). Further investigations are necessary not only to increase the knowledge of the tree frog diversity in the region but also to clarify the distribution range of recently described species reported from neighbouring countries to create corresponding conservation measures or to adapt existing ones.

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