



A new species of the genus *Odorrana* (Amphibia: Ranidae) and the first record of *Odorrana bacboensis* from China

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Abstract

The genus *Odorrana* currently contains at least 56 recognized species that inhabits montane streams in subtropical and tropical Asia. Twenty new species have been described in the last decade, indicating the potential cryptic species diversity of this genus. We collected several specimens of *Odorrana* species from Southern China from 2007 to 2014, and on the basis of a combined morphological characters and phylogenetic analysis, we described the new species *Odorrana fengkaiensis* sp. nov. herein. The new species is very similar to *O. hainanensis* and *O. bacboensis*, but can be consistently separated by morphology, and allopatric distribution. It is further reciprocally monophyletic to *O. hainanensis* in a mitochondrial gene trees with an average genetic divergence of 2.1% (1.9%–2.4%). The new species inhabits in lowland broad streams, rivers, pools and near the riparian areas, but its general ecology remains poorly known. The new species is characterized by its body length of adult females approximately twice as long as adult males (SVL 77.8–111.9 mm in females, 37.4–51.8 mm in males); eye large in males, eye diameter 1.01–1.16 times as long as snout length; tympanum of males large and distinct, extremely close to the eye, 0.7–1.4 mm in tympanum-eye distance; dorsolateral folds absent; dorsal skin shagreened, with several large tubercles in males; flanks with tubercles and scattered larger pustules, 8–10 of which usually arranged in a dorsolateral row; ventral skin smooth, with spines in adult males during the breeding season; the tibio-tarsal articulation stretched forward beyond the tip of snout; relative finger lengths: II < I < IV < III; dorsum brown with irregularly reticulated green markings in males and young females, uniformly brown in some old adult females; males with velvety nuptial pad on thumb, paired gular pouches; mature oocytes almost purely black in life, showed dark grey animal pole and olive vegetative pole in preservative. In addition, we found *O. bacboensis*, a new country record from China, indicating a range extension from north-central Vietnam to southeast Yunnan and adjacent area in Guangxi.

Key words: China, *Odorrana*, 16s rRNA, 12s rRNA, morphology, taxonomy

Introduction

The genus *Odorrana* Fei *et al.* (1990) has been widely recognized as a well-supported monophyletic group on the basis of molecular phylogenetic analyses (Matsui *et al.* 2005; Ngo *et al.* 2006; Cai *et al.* 2007; Che *et al.* 2007; Stuart 2008). According to Frost (2015), the genus *Odorrana* currently contains at least 56 recognized species and is widely distributed in montane streams and rivers in subtropical and tropical regions of East and Southeast Asia, ranging from the Ryukyu Archipelago in Japan, southern China, Indochina, northeastern India, Thai-Malay Peninsula and southwards to Sumatra and Borneo.

Most species of *Odorrana* inhabit montane rivers or streams. This peculiar ecological niche may promote inter- or intra- specific divergence through geographical isolation, especially given the species complex with a wide geographical range covering varied mountain ranges and variable habitats. Indeed, many cryptic species of *Odorrana* have been discovered. For example, 20 new species of *Odorrana* have been described in the last decade (Stuart & Chan-ard 2005; Stuart *et al.* 2005; Bain & Stuart 2006; Stuart & Bain 2005, 2006; Matsui &

Jaafar 2006; Orlov *et al.* 2006; Stuart *et al.* 2006; Li *et al.* 2008; Tran *et al.* 2008; Yang 2008; Yang & Rao 2008; Bain *et al.* 2009; Fei *et al.* 2009; Chen *et al.* 2010a, 2010b; Kuramoto *et al.* 2011; Mo *et al.* 2015). This indicates further discoveries or potential taxonomic changes are very likely in this genus.

Taxonomically, many species of the genus *Odorrana* are not easily identified owing to subtle interspecific morphological differences. Therefore, other evidence such as molecular genetics and bioacoustics may be necessary. From 2007 to 2014, we carried out series biodiversity surveys to sample herpetofauna in Southeast China, a region with underestimated herpetological diversity (Li *et al.* 2014; Wang *et al.* 2013, 2014), and ongoing conservation threats (Karraker *et al.* 2010). We collected a number of specimens of *Odorrana* superficially resembling *O. bacboensis* and *O. hainanensis*, which are potentially distributed in this region and adjacent areas. Morphologically, these species are very close to each other and we thus used an integrative taxonomy approach by combining molecular phylogenetic analyses and morphological characters to distinguish the differences of these specimens. Our results revealed an undescribed *Odorrana* species from Guangdong and Guangxi represent as a new species. We also discovered *Odorrana bacboensis*, a new amphibian record to China.

Material and methods

Taxon sampling. We analysed a total of 30 samples from 21 localities, which represent unnamed taxon and all of currently recognized species of genus *Odorrana* without dorsolateral fold from southern China and adjacent area. Among them, DNA samples of unnamed *Odorrana* species were collected from Fengkai County, Guangdong, Jingxi County, Shangsi County and Napo County, Guangxi and 12 recognized species, including *O. hainanensis*, *O. jingdongensis*, *O. huangshanensis*, *O. tianmuisi*, *O. margaretae*, *O. wuchuanensis*, *O. yizhangensis* and *O. lungshengensis*, were collected during our field work (for localities see Fig. 1). DNA sequences of other species (*O. bacboensis*, *O. tiannanensis*, *O. andersonii* and *O. sckmackeri*) were obtained from GenBank. Sequence of *Hylarana guentheri* was used as outgroup. Data of all voucher specimens and associated GenBank accession numbers of above species are available in Table 1.

DNA Extraction, PCR amplification and sequencing. DNA was extracted from liver tissue using a standard phenol-chloroform extraction protocol (Sambrook *et al.* 1989). We sequenced the 16S rRNA and 12S rRNA of mitochondrial genes from our 21 samples. Fragments of the two genes were amplified using the primer pairs designed for ranid frogs (Sumida & Ogata 1998; Sumida *et al.* 2000). PCR amplification reactions were performed in a 30 volume reaction with the following cycling conditions: an initial denaturing step at 95°C for 4 min; 35 cycles of denaturing at 95°C for 40 s, annealing at 55°C (for 16S rRNA) or 53°C (for 12S rRNA) for 40 s and extending at 72°C for 60 s, and a final extending step of 72°C for 10 min. PCR products were purified with spin columns. The purified products were sequenced with both forward and reverse primers using BigDye Terminator Cycle Sequencing Kit according to the guidelines of the manufacturer. The products were sequenced an ABI Prism 3730 automated DNA sequencer in ShangHai Majorbio Bio-pharm Technology Co. Ltd.. All sequences have been deposited in GenBank. Some homologous DNA sequences of voucher specimen of related species were downloaded from GenBank and incorporated into further phylogenetic analyses (Table 1).

Phylogenetic analyses. Sequences were assembled and aligned using MEGA 6.06 (Tamura *et al.* 2013) and the resulting alignment was checked by eye and revised manually if necessary. Considering all mtDNA gene sequences are effectively inherited as one locus, the two mitochondrial gene segments were concatenated into a single partition for the analyses. The General Time-Reversible (GTR) model (Posada & Crandall 2001) assuming a gamma-shaped distribution across sites (Felsenstein 2004) was selected as the best-fitting nucleotide substitution model using the Akaike Information Criterion (Akaike 1974) in Modeltest 3.7 (Posada *et al.* 2004). The sequence data were analyzed using maximum likelihood (ML) implemented in MEGA 6.06 (Tamura *et al.* 2013), and Bayesian Inference (BI) in MrBayes 3.12 (Ronquist & Huelsenbeck 2003). For ML analysis, the bootstrap consensus tree inferred from 1000 replicates was used to represent the evolutionary history of the taxa analyzed (Felsenstein 1985). Branches corresponding to partitions reproduced in less than 50% bootstrap replicates are collapsed. For BI analysis, two independent runs with four Markov Chains Monte Carlo chains were performed for one million generations and sampled every 100th generation. The first 25% of samples were discarded as burn-in. Apart from phylogenetic tree-based methods, we also calculated row pairwise sequence divergence using on Kimura-2-parameter (K2P) divergences implemented in MEGA.

TABLE 1. Samples of our collection and voucher specimens used in this study.

ID	Species	Specimen voucher no.	Localities	12s rRNA	16S rRNA
1	<i>Odorrana fengkaiensis</i> sp. nov.	SYS a002262	China: Heishiding Nature Reserve, Fengkai Co., Guangdong	KT315354	KT315375
2	<i>Odorrana fengkaiensis</i> sp. nov.	SYS a002263	China: Heishiding Nature Reserve, Fengkai Co., Guangdong	KT315355	KT315376
3	<i>Odorrana fengkaiensis</i> sp. nov.	SYS a002273	China: Heishiding Nature Reserve, Fengkai Co., Guangdong	KT315356	KT315377
4	<i>Odorrana fengkaiensis</i> sp. nov.	SYS a002160	China: Heishiding Nature Reserve, Fengkai Co., Guangdong	KT315357	KT315378
5	<i>Odorrana fengkaiensis</i> sp. nov.	SYS a002161	China: Heishiding Nature Reserve, Fengkai Co., Guangdong	KT315358	KT315379
6	<i>Odorrana fengkaiensis</i> sp. nov.	SYS a002253	China: Tongling Canyon, Jingxi Co., Guangxi	KT315359	KT315380
7	<i>Odorrana fengkaiensis</i> sp. nov.	SYS a001045	China: Tongling Canyon, Jingxi Co., Guangxi	KT315360	KT315381
8	<i>Odorrana fengkaiensis</i> sp. nov.	SYS a001025	China: Shiwandashan Nature Reserve, Shangsi Co., Guangxi	KT315361	KT315382
9	<i>Odorrana hainanensis</i>	SYS a002260	China: Diaoluoshan Forest Park, Lingshui Co., Hainan	KT315362	KT315383
10	<i>Odorrana hainanensis</i>	SYS a000636	China: Diaoluoshan Forest Park, Lingshui Co., Hainan	KT315363	KT315384
11	<i>Odorrana bacboensis</i>	ROM 13044	Vietnam: Nghe An: Khe Moi	AF206099	AF206480
12	<i>Odorrana bacboensis</i>	SYS a001046	China: Baiman village, Napo Co., Guangxi	KT315364	KT315385
13	<i>Odorrana andersonii</i>	HNNU001YN	China: Longchuan Co., Yunnan	KF185021	KF185057
14	<i>Odorrana jingdongensis</i>	20070711017	China: Jingdong Co., Yunnan	KF185014	KF185050
15	<i>Odorrana jingdongensis</i>	SYS a002995	China: Ailaoshan Nature Reserve, Zhenyuan Co., Yunnan	KT315365	KT315386
16	<i>Odorrana schmackeri</i>	HNNU 0908_349	China: Yichang City, Hubei	KF185011	KF185047
17	<i>Odorrana huanggangensis</i>	SYS a001612	China: Mt. Huanggangshan, Yanshan Co., Jiangxi	KT315366	KT315387
18	<i>Odorrana huanggangensis</i>	SYS a001724	China: Sangang Village, Wuyishan City, Fujian	KT315367	KT315388
19	<i>Odorrana huanggangensis</i>	SYS a002817	China: Nanling Nature Reserve, Ruyuan Co., Guangdong	KT315368	KT315389
20	<i>Odorrana tianmii</i>	SYS a002680	China: Mt. Tianmu, Lian'an Co., Zhejiang	KT315369	KT315390
21	<i>Odorrana margaretae</i>	SYS a003214	China: Mt. Qingchengshan, Dujiangyan City, Sichuan	KT315370	KT315391
22	<i>Odorrana margaretae</i>	SYS a002317	China: Jianshi Co., Hubei	KT315371	KT315392
23	<i>Odorrana wuchuanensis</i>	SYS a002321	China: Jianshi Co., Hubei	KT315372	KT315393
24	<i>Odorrana yizhangensis</i>	SYS a001870	China: Mt. Jinggong, Jiangxi	KT315373	KT315394
25	<i>Odorrana lungshengensis</i>	SYS a002229	China: Leigongshan Nature Reserve, Leishan Co., Guizhou	KT315374	KT315395
26	<i>Odorrana tiannanensis</i>	HNNU HK001	China: Hekou, Yunnan	KF185008	KF185044
27	<i>Odorrana tiannanensis</i>	ROM 7038	Vietnam: Pac Ban	AF206105	AF206486
28	<i>Odorrana tiannanensis</i>	ROM 13046	Vietnam: Khe Moi	AF206100	AF206481
29	<i>Odorrana tiannanensis</i>	SCUM50510CHX	China: Hekou, Yunnan	EF453736	EF453751
30	<i>Hylarana guentheri</i>	HNNU 0604325	China: Fuzhou, Fujian	KF185024	KF185060

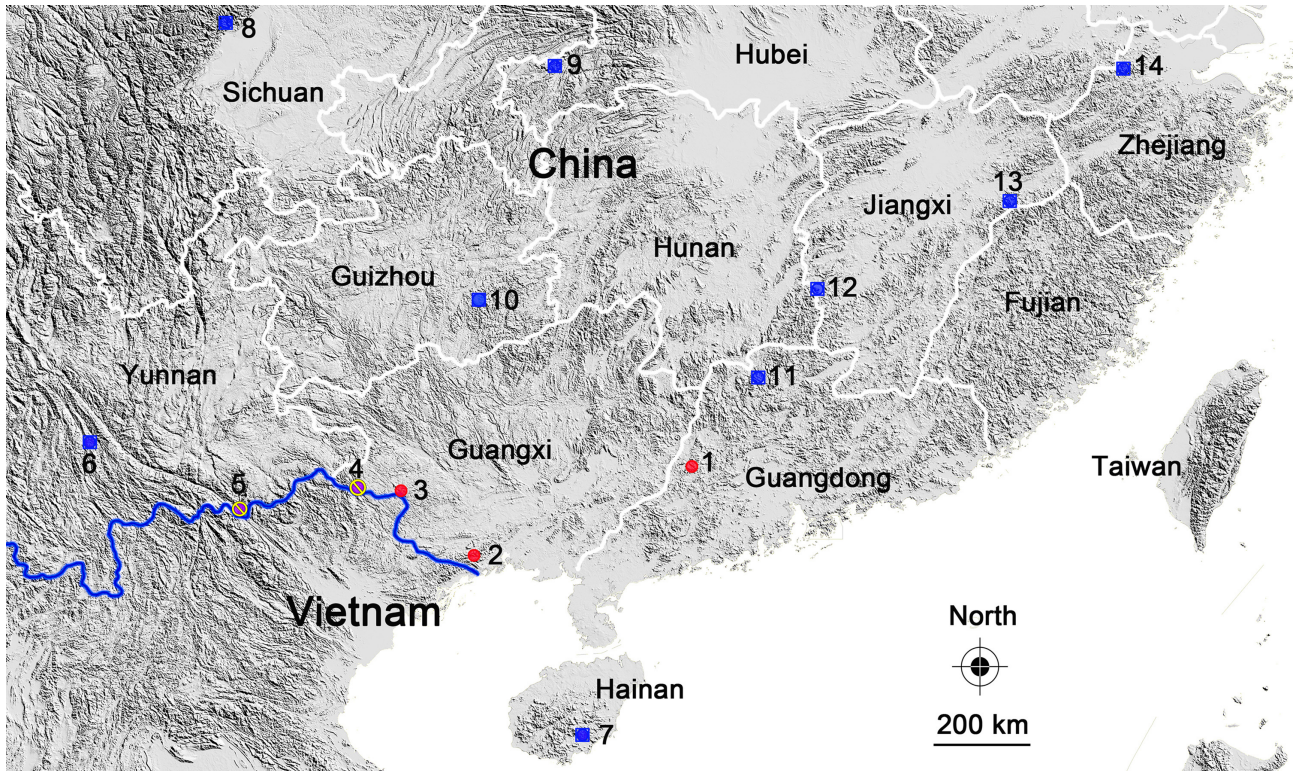


FIGURE 1. Sampling localities in southern China. Three red marks represent the collecting localities of *O. fengkaiensis* sp. nov., (1) type locality: Heishiding Nature Reserve, Fengkai County, Guangdong Province; (2) Shiwandashan Nature Reserve, Shangsi County, Guangxi; (3) Tongling Canyon, Xinling Village, Jingxi County, Guangxi. Two violet marks represent the sampling localities of *O. bacboensis*, (4) Bainan Village, Napo County, Guangxi, and (5) Hekou County, Yunnan. (6): Ailaoshan Nature Reserve, Zhenyuan County, Yunnan, specimen collected here refers to *O. jingdongensis*. (7): Diaoluoshan Forest Park, Lingshui County, Hainan, specimens collected here refer to *O. hainanensis*. (8): Mt. Qingchengshan, Dujiangyan City, Sichuan, specimen collected here refers to *O. margaretae*. (9): Jianshi County, Hubei, specimens collected here refer to *O. margaretae* and *O. wuchuanensis*, respectively. (10): Leigongshan Nature Reserve, Leishan County, Guizhou, specimen collected here refers to *O. lungshengensis*. (11): Nanling Nature Reserve, Ruyuan County, Guangdong and (13): Mt. Wuyi, Jiangxi and Fujian Provinces, specimens collected in localities refer to *O. huangshanensis*. (12): Mt. Jinggang, Jiangxi, specimen collected here refers to *O. yizhangensis*. (14): Mt. Tianmu, Lian'an County, Zhejiang, specimen collected here refers to *O. tianmuui*.

Morphological characters. Measurements were taken with digital calipers to the nearest 0.1 or 0.01 mm. Abbreviations used are SVL = snout-vent length; HDL = head length from tip of snout to the articulation of the jaw; HDW = head width, between left and right articulations of the quadratojugal and maxilla; SNT = snout length, from tip of snout to the anterior corner of the eye; ED = eye diameter, from the anterior corner of the eye to posterior corner of the eye; IND = internasal distance; IOD = interorbital distance; TYD = tympanum diameter; TED = tympanum–eye distance, from anterior edge of tympanum to posterior corner of the eye; HND = hand length, from distal end of radioulna to tip of distal phalanx of finger III; TIB = tibia length; FTL = foot length from distal end of tibia to tip of distal phalanx of IV; FPW = finger disk width, at the widest part of the pad of III; DPW = width of distal phalanx of III. All specimens were measured by Ying-Yong Wang.

Collection Abbreviations: **CIB**, Chengdu Institute of Biology, the Chinese Academy of Sciences, Chengdu, China; **FMNH**, The Florida Museum of Natural History, Chicago, USA; **HNNU**, Zoological Museum of Henan Normal University, Xinxiang, China; **KIZ**, Kunming Institute of Zoology, Kunming, China; **ROM**, Royal Ontario Museum, Toronto, Canada; **SCUM**, Zoological Museum of Sichuan University, Chengdu, China; **SYS**, The Museum of Biology, Sun Yat-sen University, Guangzhou, China.

Results

The Maximum likelihood (ML) and Bayesian inference (BI) phylogenetic trees were constructed based on concatenated DNA sequences of the mitochondrial 12S rRNA (745-bp) and 16S rRNA (996-bp) gene with a total length of 1741-bp. Two analyses resulted in essentially identical topologies with strong node supporting values. The phylogeny tree (Fig. 2) indicates that 29 samples of *Odorrana* have been divided into three strongly supported basal lineages, designated here as the Clade A (BPP = 1.00, BS = 95), Clade B (BPP = 0.98, BS = 79) and the Clade C (BPP = 0.95, BS = 84). Clade A is composed of two recognized sister species: *O. yizhangensis* and *O. lungshengensis*. Clade B is composed of four recognized species: *O. wuchuanensis*, *O. margaretae*, *O. andersonii* and *O. jingdongensis*; the pairwise genetic distance between *O. jingdongensis* and *O. andersonii* was 0.024 (K2P distance), see Table 2.

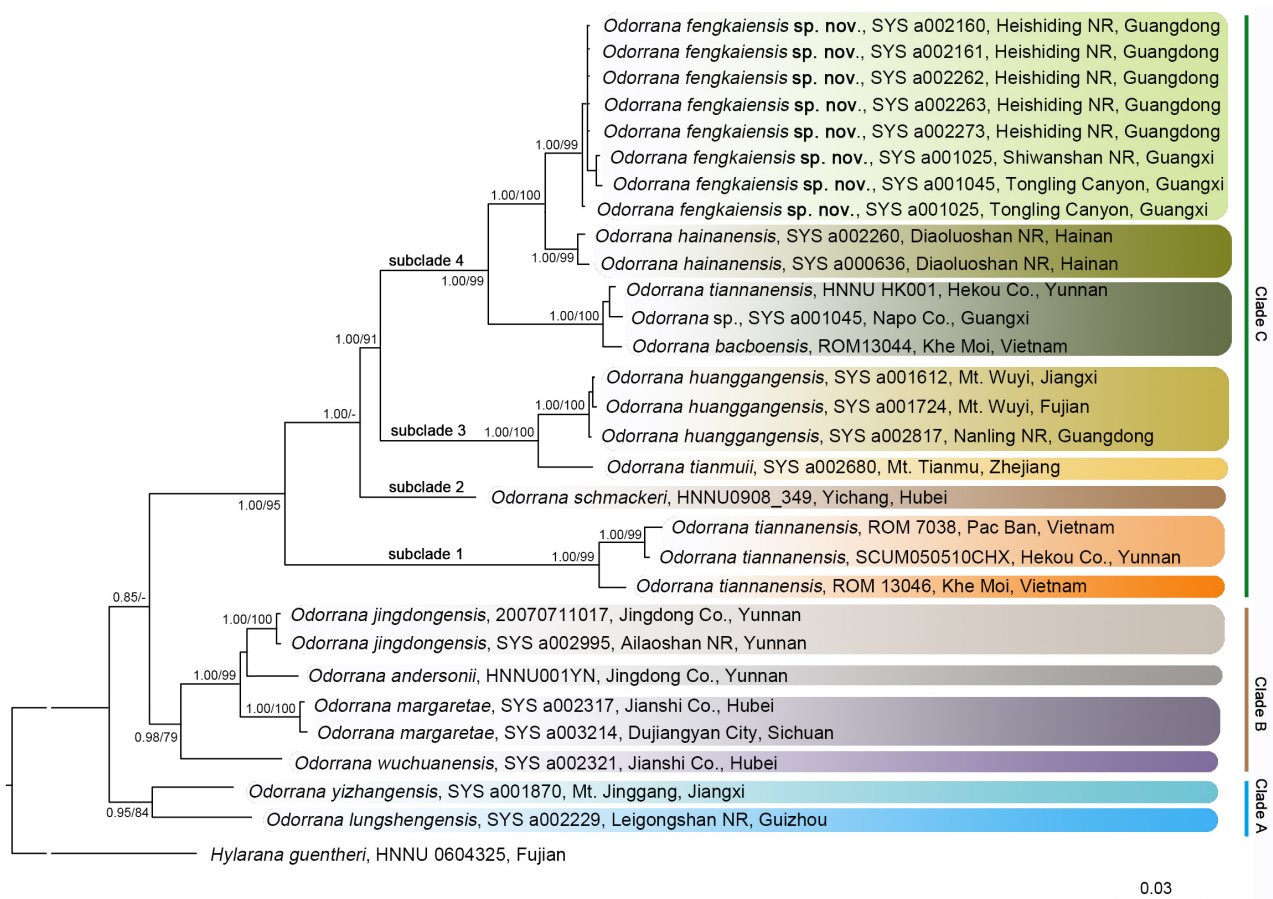


FIGURE 2. Bayesian inference tree derived from partial DNA sequences of the mitochondrial 12S rRNA and 16S rRNA gene with Bayesian posterior probabilities (BPP>80% retained) and maximum-likelihood bootstrap values (500 replicates; BS>60 retained), respectively.

All members of Clade C were further divided into four major, deeply divergent, and strongly supported monophyletic subclades. Subclade 1 contains three specimens designated as *O. tiannanensis* from Hekou County, Yunnan, China and Vietnam. Subclade 2 consists of *O. schmackeri* collected from the species' type locality. Subclade 3 consists of two species, which were previously designated as *Odorrana schmackeri* and recently described as *O. huanggangensis* and *O. tianmuyii*.

In subclade 4, eight specimens from Fengkai County of Guangdong, Shangsi and Jingxi Counties of Guangxi, were grouped together with a small genetic variation to each other (<0.001, see Table 2), and reciprocal monophyly to *O. hainanensis* with a moderate mtDNA sequence divergence (pairwise genetic distance were 0.019–0.024, which were at a same divergence level between *O. jingdongensis* and *O. andersonii* was 0.024, see Table 2). Therefore, the taxon of genus *Odorrana* from the Fengkai County, Guangdong, Shangsi and Jingxi Counties, Guangxi, China, represents a distinct undescribed species, which is described below as a new species, *Odorrana fengkaiensis* sp. nov..

TABLE 2 Genetic divergence of the *Odorrana* based on Kimura-2-parameter (K2P) divergences (%). Among them, *Odorrana fengkaiensis* sp. nov.: SYS a002262 (1), SYS a002263 (2), SYS a002273 (3), SYS a002160 (4) and SYS a002161 (5) from Heishiding Nature Reserve, Guangdong; SYS a002253 (6) and SYS a001045 (7) from Tongling Canyon, Jingxi Co., Guannxi; SYS a001025 (8) from Shiwandashan Nature Reserve, Shangsi Co., Guangxi. *Odorrana hainanensis*: SYS a002260 (9) and SYS a000636 (10) from Diaoloshan Nature Reserve, Hainan. *Odorrana bachoensis*: ROM 13044 (11) from Khe Moi, Vietnam, SYS a001046 (12) from Napo Co., Guangxi. *Odorrana andersoni*: HNNU001YN (13) from Longchuan Co., Yunnan. *Odorrana jingdongensis*: 20070711017 (14) from Jingdong Co., Yunnan, SYS a002995 (15) from Ailaoshan Nature Reserve, Zhenyuan Co., Yunnan; *Odorrana schmackeri*: HNNU 0908_349 (16) from Yichang City, Hubei; *Odorrana huanggangensis*: SYS a001612 (17) and SYS a001724 (18) from Wuyi Mountains, Yanshan Co. of Jiangxi and Wuyishan City of Fujian, respectively, SYS a002817 (19) from Nanling Nature Reserve, Ruyuan Co., Guangdong; *Odorrana tiannanensis*: SYS a002680 (20) from Lin'an City, Zhejiang; *Odorrana margaritae*: SYS a003214 (21) and SYS a002317 (22) from Duijiangyan City, Sichuan and Jianshi Co., Hubei, respectively; *Odorrana wuchuanensis*: SYS a002321 (23) from Jianshi Co., Hubei; *Odorrana yizhangensis*: SYS a001870 (24) from Mt. Jiangan, Jiangxi; *Odorrana lungshengensis*: SYS a002229 (25) from Mt. Leigong, Guizhou; *Odorrana tiannanensis*: HNNU HK001 (26) and SCUM50510CHX (29) from Hekou, Yunnan, ROM 7038 (27) and ROM 13046 (28) from Pac Ban and Khe Moi, Vietnam, respectively; *Hylarana gaitheri*: HNNU 0604325 (30) from Fuzhou City, Fujian.

	1-5	6-7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	
1-5																									
6-7	0.001																								
8	0.000	0.001																							
9	0.020	0.019	0.020																						
10	0.024	0.023	0.024	0.004																					
11	0.055	0.053	0.055	0.058	0.063																				
12	0.053	0.052	0.053	0.058	0.063	0.007																			
13	0.141	0.143	0.141	0.142	0.134	0.139	0.134																		
14	0.141	0.139	0.141	0.141	0.134	0.128	0.121	0.021																	
15	0.141	0.139	0.141	0.141	0.134	0.128	0.121	0.021	0.000																
16	0.081	0.079	0.081	0.078	0.075	0.074	0.073	0.117	0.119	0.119															
17	0.092	0.093	0.092	0.095	0.089	0.095	0.094	0.122	0.115	0.115	0.079														
18	0.093	0.095	0.093	0.097	0.090	0.097	0.096	0.124	0.116	0.116	0.081	0.001													
19	0.092	0.093	0.092	0.095	0.089	0.095	0.094	0.122	0.115	0.115	0.079	0.000	0.001												
20	0.092	0.090	0.092	0.097	0.090	0.096	0.090	0.119	0.111	0.111	0.078	0.028	0.029	0.028											
21	0.153	0.151	0.153	0.154	0.146	0.147	0.140	0.024	0.023	0.023	0.126	0.138	0.140	0.138	0.127										
22	0.153	0.151	0.153	0.154	0.146	0.147	0.140	0.024	0.023	0.023	0.126	0.134	0.136	0.134	0.127	0.002									
23	0.133	0.131	0.133	0.128	0.121	0.137	0.131	0.051	0.046	0.046	0.113	0.111	0.113	0.111	0.106	0.054	0.054								
24	0.142	0.144	0.142	0.137	0.129	0.141	0.137	0.078	0.071	0.071	0.125	0.135	0.137	0.135	0.129	0.080	0.080	0.065							
25	0.129	0.127	0.129	0.123	0.116	0.126	0.125	0.081	0.074	0.074	0.113	0.118	0.120	0.118	0.112	0.083	0.083	0.072	0.046						
26	0.052	0.051	0.052	0.057	0.062	0.006	0.003	0.131	0.121	0.121	0.070	0.094	0.096	0.094	0.087	0.136	0.136	0.128	0.136	0.123					
27	0.140	0.142	0.140	0.147	0.143	0.158	0.158	0.157	0.179	0.179	0.132	0.133	0.135	0.133	0.139	0.175	0.171	0.151	0.167	0.160	0.155				
28	0.128	0.130	0.128	0.135	0.131	0.143	0.144	0.136	0.157	0.157	0.115	0.126	0.128	0.126	0.125	0.153	0.153	0.133	0.148	0.141	0.140	0.014			
29	0.134	0.136	0.134	0.141	0.137	0.151	0.152	0.148	0.170	0.170	0.126	0.129	0.131	0.129	0.135	0.166	0.162	0.143	0.158	0.151	0.148	0.005	0.011		
30	0.208	0.208	0.208	0.228	0.223	0.243	0.242	0.207	0.214	0.214	0.213	0.207	0.209	0.207	0.203	0.210	0.210	0.188	0.214	0.193	0.239	0.221	0.214	0.216	

Another three specimens in subclade 4, ROM 13044 noted as *O. bacboensis* from its type locality Khe Moi, Vietnam, HNNU HK001 noted as *O. tiannanensis* (Chen *et al.* 2013) from Hekou County, Yunnan, and SYS a001046 from Napo County, Guangxi, were grouped together with a small genetic distance (0.007, see Table 2) and represented the same taxon. The population from Napo County, Guangxi, China, should be identified as *O. bacboensis* on the basis of the following characters: gravid females (SYS a001046 and 1047) possessed black mature oocytes as opposed to pure yellow in *O. tiannanensis* in life (Yang & Li 1990; Fei *et al.* 2009, 2012), absent pectoral spines in adult male (SYS a001048) as opposed to present pectoral spines in *O. hainanensis* and *O. fengkaiensis*. Therefore, they were identified as *O. bacboensis* and thus our finding, representing the populations from Napo and Hekou Counties was the first record of *O. bacboensis* in China.

***Odorrana fengkaiensis* sp. nov.**

Figs. 3, 4

Holotype. SYS a002265 (Fig. 3), adult male, from Heishiding Nature Reserve (23°27'40.16" N, 111°54'32.80" E; 253 m a.s.l.), Fengkai County, Guangdong Province, China, collected by Ying-Yong Wang (YYW hereafter).

Paratypes. A total of 41 specimens (10 adult males, 31 adult females): 32 specimens from the same locality as the holotype at elevations between 190–510 m a.s.l. by YYW, Jian-Huan Yang (JHY hereafter), Yu-Long Li (YLL hereafter), Jian Zhao (JZ hereafter) and Run-Lin Li (RLL hereafter): 10 adult males, SYS a000174, SYS a000175 and SYS a000176 (Fig. 4: B) collected on 2nd May 2008, SYS a000179 and SYS a000181 on 30th May 2008, SYS a000185 on 31st May 2008, SYS a000413 on 15th July 2008, SYS a000792 on 13th May 2010; SYS a001880 on 28th June 2012, SYS a002263 on 12th August 2013; 22 adult females, SYS a000105, 0106 (Fig. 4: Fe), 0108, 0110, 0111, 0112, 0127 and 0128, collected on 10th–20th July 2007, SYS a000182, 0183 (Fig. 4: B) on 2nd May 2008, SYS a000184 on 29th May 2008, SYS a000143 on 23rd March 2008, SYS a000790 and 0791 on 13th May 2010, SYS a000793 on 26th May 2010, SYS a001879 and 1881 on 28th June 2012, SYS a002160 and 2161 on 2nd June 2013, SYS a002262 (Fig. 4: D) on 13th August 2013; SYS a002273 on 19th August 2013, SYS a003345 on 3rd October 2014. Two adult females from Shiwandashan Forest Park (21° 54' 16.36" N, 107° 54'11.15" E; at elevations between 292–310 m a.s.l.), Shangsi County, Guangxi, SYS a001025 (Fig. 4: F) on 3rd August 2010, SYS a001352 on 16th August 2011. Seven adult females from Tongling Canyon (23°0'11.07"N, 106°40'2.22"E; 450–550 m a.s.l.), Jingxi County, Guangxi Zhuang Autonomous Region, China by JHY, YLL, JZ and RLL: SYS a001043, 1044 and 1045 on 4–6th August 2010, SYS a001366, 1367, 1368 on 20th–21st August 2011, SYS a002253 on 22nd July 2013.

Diagnosis. *Odorrana fengkaiensis* sp. nov. can be distinguished from other congeners by the following characters: (1) the body length of adult females approximately twice as long as males (SVL 77.8–111.9 mm in females, 37.4–51.8 mm in males); (2) eye large in males, longer than snout length, ED:SNT ratio 1.01–1.16; (3) tympanum of males large and distinct, extremely close to the eye, 0.7–1.4 mm in tympanum–eye distance (TED); (4) supratympanic fold slightly distinct; (5) dorsolateral folds absent; (6) dorsal skin shagreened with dense granules, only males with several large tubercles on dorsum; (7) flanks with tubercles and scattered larger pustules, 8–10 of which usually arranged in a dorsolateral row; (8) venter smooth; ventral spines present in adult males during the breeding season; (9) the heels significant overlapping, tibio-tarsal articulation stretched forward beyond the tip of snout; (10) disks on digits cordiform, pointed and moderately enlarged, FPW:DPW ratio 1.16–1.52 in males, 1.14–1.57 in females; (11) disks of all digits with circum-marginal grooves; (12) relative finger lengths: II < I < IV < III; (13) feet fully webbed; (14) dorsum brown with irregularly reticulated green markings in males and young females, uniformly brown in some old adult females; dorsal limbs and digits brown with black transverse bands; (15) males with velvety nuptial pad on thumb, paired gular pouches; (16) mature oocytes purely black in life, animal pole dark grey and vegetative pole olive in preservative.

Description of holotype. Size moderate (SVL 51.2 mm); head longer than wide (HDL:HDW = 1.16); snout slightly long (SNT:HDL = 0.41), obtusely rounded in dorsal view, rounded in profile, projecting beyond lower jaw; eye large and convex, eye diameter (ED) 1.03 times of snout length (SNT), upper eyelid wider than interorbital distance; top of head flat; canthus rostralis rounded; lip flared; loreal region concave; internasal distance (IND 5.2 mm) larger than interorbital distance (IOD 4.0 mm); tympanum circular, large, distinctly visible, 0.54 times of eye diameter; tympanum–eye distance small (TED 1.1 mm, TED:TYD = 0.25); tympanic rim elevated relative to skin

of temporal region; choanae large, semicircular or inverted triangular, partly concealed by the maxillary shelves; two vomerine ridges markedly elevated, oblique, posteromedial to choanae, separated by a distance barely equal to length of one, bearing prominent teeth; tongue deeply notched posteriorly; paired gular pouches at corners of throat.



FIGURE 3. The holotype SYS a002265 of *Odorrana fengkaiensis* sp. nov.. **A:** dorsal view in life; **B:** ventral view in life; **C:** ventral spinules; **D:** dorsal view of hand; **E:** ventral view of hand; **F:** ventral view of foot. Photos by YLL and YYW.



FIGURE 4. Variation in morphology and colour pattern of *Odorrana fengkaiensis* sp. nov. in life. **A:** dorsolateral view of an adult male; **B:** dorsolateral view of an adult male (SYS a000176) and a gravid young female (SYS a000183); **C:** dorsal view of male froglet; **D:** dorsolateral view of a gravid young female (SYS a002262); **E:** an old adult female found on 3rd November, 2012; **F:** SYS a001045, an gravid old female from Tongling Canyon, Guangxi. Photos by YYW and JHY.

Forelimbs moderately robust, hand moderately long, hand length (HDL) 0.3 times of SVL; fingers slender, relative finger lengths $II < I < IV < III$; fingers free of webbing, tips of fingers moderately dilated, becoming pointed, cordiform disks; width of disk slightly larger than width of distal phalanx of finger III, $FPW:DPW = 1.18$; terminal phalanges T-shaped; lateroventral circummarginal grooves not meeting at the tip of disks; subarticular tubercles ovoid, markedly elevated and prominent; supernumerary tubercle below the base of each finger, distinct,

significantly smaller than subarticular tubercles; metacarpal tubercle three, inner one elongated and oblong, other two small and indistinct. Hindlimbs robust, relatively long; tibio-tarsal articulation beyond the tip of snout when hindlimb adpressed along the side of the body; heels overlapped when the flexed hindlimbs held at right angles to the body axis; tibia length (TIB) 0.55 times of SVL; foot length (FTL) 0.78 times of SVL; toes long, slender, relative toe lengths $I < II < III < V < IV$; tips of toes slightly dilated, becoming narrow and long triangular disks; circummarginal grooves present; feet fully webbed to disks; free edges of toes I and V with wide lateral fringes; subarticular tubercles prominent, ovoid; inner metatarsal tubercle elongated, ellipsoid; outer metatarsal tubercle absent; inner tarsal fold absent.

Skin on dorsum shagreened with dense granules; a number of pustules scattered on flanks and dorsum of trunk, eight large pustules forming a longitudinal row; dorsolateral folds absent; supratympanic folds slightly prominent, from posterior corner of eye, curving posteroventrally, extending to a level above insertion of arm; two rictal glands, the anterior one continuous with upper lip and the posterior one above insertion of arm and continuous with supratympanic fold; venter smooth with ventral spinules; distinct granules present on posterior thighs and around cloaca; cloacal opening unmodified, directed posteriorly, at upper level of thighs.

Measurements of holotype (in mm). SVL 51.2, HDL 19.5, HDW 16.8, SNT 7.9, IND 5.2, IOD 4.0, ED 8.1, TYD 4.4, TED 1.1, HND 15.5, FTL 40.1, TIB 28.0, FPW 1.00, DPW 0.85.

Coloration in life. Dorsum of head and body brown with large dark-brown spots, and reticulated green markings anterior to sacral vertebra; upper part of flank brown, lower part of flank light yellow with several large black spots; upper and lower lips brownish yellow with vertical black bars, the one under the eye largest and distinct; rictal glands brownish yellow; dorsal surface of limbs brown with black transverse bands; posterior surface of thigh brown with black and yellowish irregular markings; webbing on feet dark brown with yellowish marking; ventral surface white to yellowish, chest and chin mottled with light-brown blotches; pupil black edged with a striking bright yellow border; iris brown-yellow with black blotches and dense tiny freckles.

Coloration in preservative. Dorsum, flanks and limbs dark-brown, dorsum with large blackish spots; ventral surface of body and limbs creamy white with faint brown spots on chest and chin.

Variation. Measurements and body proportions of type series of *Odorrana fengkaiensis* **sp. nov.** are given in Table 3.

The new species shows obvious differences among females and males. SVL of adult females approximately twice as long as of males, the body size of female individuals from Shiwandashan Nature Reserve and Tongling Canyon, Guangxi, significantly greater than from Heishiding Nature Reserve, Fengkai County, Guangdong (SVL of adult females 89.0–111.9 (103.1 ± 7.8) mm from Shangsi and Jingxi, Guangxi; 77.3–109.9 (93.2 ± 8.9) mm from Heishiding Nature Reserve, Guangdong). Dorsum of young adult females garnished with reticulated green to light-green markings (Fig. 4: B and D), but in some old adult female individuals (Fig. 4: E and F), the dorsum uniform brown without green pattern. In froglet (Fig. 4: C), the whole body olive, dorsum with brown irregular spots. Disks of digits of female individuals from Guangxi are larger than from Heishiding Nature Reserve (FPW/DPW ratio 1.79–1.94 vs. 1.35–1.80). Moreover, males with velvety nuptial pad on finger I, paired gular pouches; mature oocytes in life almost purely black (SYS a000111, SYS a00184, SYS a002161, SYS a002262), in preservative showed dark grey animal pole and olive vegetative pole.

Comparisons. Comparative data of *O. fengkaiensis* **sp. nov.** with 56 recognized species of the genus *Odorrana* were obtained from the literature (Ao *et al.* 2003; Bain *et al.* 2003, 2009; Bain and Stuart 2006; Fei *et al.* 2001, 2009, 2012; Li *et al.* 2008; Matsui 1994; Matsui & Jaafar 2006; Mo *et al.* 2015; Orlov *et al.* 2003, 2006; Stuart *et al.* 2005, 2006, Stuart & Bain 2005; Tung *et al.* 2008; Yang & Li 1990). Examined specimens of *O. versabilis*, *O. nasuta*, *O. exiliversabilis*, *O. graminea*, *O. tormota*, *O. zhaoi*, *O. hainanensis*, *O. margaretae*, *O. jingdongensis*, *O. huangshanensis*, *O. schmackeri*, *O. tianmuyii*, *O. lungshengensis*, *O. wuchuanensis* and *O. yizhangensis* are listed in the Appendix 1.

Odorrana fengkaiensis **sp. nov.** is most similar to *O. bacboensis*, *O. hainanensis* and *O. tiannanensis*. It differs from *O. hainanensis* by having relatively large eye in males, ED longer than SNT (ED: SNT ratio 1.01–1.16, median 1.09) vs. usually ED smaller than SNT, (ED:SNT 0.90–1.03, median 0.97) in *O. hainanensis*; disks on fingers of males moderately enlarged, FPW:DPW ratio 1.16–1.52 (median 1.34) vs. disks on fingers significantly enlarged, FPW:DPW ratio 1.79–1.94 (median 1.87) in *O. hainanensis* (see Fig. 7); relative finger lengths $II < I < IV < III$ vs. $II < IV < I < III$ for *O. hainanensis*; tibio-tarsal articulation forward beyond the tip of snout vs. reaches between anterior corner of the eye and tip of snout in *O. hainanensis*; mature oocytes purely black in life vs.

yellowish white with blackish brown animal pole in *O. hainanensis*. It differs from *O. bacboensis* by its eye relatively large in males, ED longer than SNT vs. ED shorter than SNT in *O. bacboensis* (ED 6.6 mm, SNT 8.8 mm in FMNH 255611 (Bain et al. 2003); ED 5.2 mm, SNT 5.8 mm in SYS a001048); disks on fingers of males moderately enlarged FPW 0.83–1.57 mm, FPW:DPW ratio 1.16–1.52 vs. disks on fingers significantly enlarged (FPW 1.8 mm in FMNH 255611 (Bain et al. 2003); FPW:DPW ratio 1.87 in SYS a001048) in *O. bacboensis*; ventral spines present in adult mature males vs. absent in *O. bacboensis*. It differs from *O. tiannanensis* by its disks of fingers moderate enlarged, (FPW 0.83–1.57 mm, median 1.20 mm) in males vs. significantly enlarged (FPW 2.0 mm), mature oocytes purely black in life vs. yellow in *O. tiannanensis*.

The absence of dorsolateral folds differentiates *O. fengkaiensis* **sp. nov.** from the following 24 congeners: *O. absita*, *O. amamiensis*, *O. banaorum*, *O. bolavensis*, *O. exiliversabilis*, *O. gigatympana*, *O. graminea*, *O. hosii*, *O. indepressa*, *O. khalam*, *O. leporipes*, *O. livida*, *O. monjerai*, *O. narina*, *O. nasica*, *O. nasuta*, *O. orba*, *O. supranarina*, *O. tormota*, *O. trankieni*, *O. utsunomiyaorum*, *O. versabilis*, *O. yentuensis* and *O. zhaoi*.

O. fengkaiensis **sp. nov.** can be distinguished from the remaining 29 recognized congeners by the combination of the following characters: dorsum brown with irregularly reticulated green markings in males and young females, becoming uniformly brown in old adult females vs. dorsal ground color always green in *O. chloronota*, *O. sinica*, *O. aureola*, *O. anlungensis*, *O. grahami*, *O. kuangwuensis*, *O. margaretae*, *O. ishikawae*, *O. splendida*, *O. huanggangensis*, *O. hejiangensis*, *O. nanjiangensis*, *O. schmackeri*, *O. tianmuyii*, *O. lipuensis*, *O. lungshengensis*, *O. wuchuanensis* and *O. yizhangensis*; body small-sized in mature males, SVL 37.4–51.8 mm vs. considerably larger in *O. cangyuanensis* (62–69 mm), *O. chapaensis* (73–83 mm), *O. geminate* (71–79 mm), *O. grahami* (70–84 mm), *O. jingdongensis* (62–82 mm), *O. mawphlangensis* (80 mm), *O. andersonii* (68–76 mm), *O. junlianensis* (73–80 mm), *O. kuangwuensis* (57 mm), *O. lungshengensis* (60–67 mm), *O. margaretae* (78–88 mm), *O. wuchuanensis* (62–77 mm); having white pectoral spinules in mature males vs. absent in *O. anlungensis*, *O. geminate*, *O. chapaensis*, *O. hejiangensis*, *O. kuangwuensis*, *O. lungshengensis*, *O. nanjiangensis*, *O. chloronota*, *O. sinica*, *O. aureola*; present paired gular pouches in males vs. absent in *O. lipuensis*, *O. margaretae* and *O. wuchuanensis*; the absence of spinules along the dorsum of body and hindlimbs, flanks of trunk, temporal region and upper lip in mature males vs. the presence of spinules along lateral surface of head, extending to posterior dorsum of body in *O. andersonii*, on dorsal surface of hindlimbs in *O. anlungensis*, from jaw angle to level of loreal region in *O. chapaensis*; on upper lip from snout tip to level of mid-portion of eye in *O. geminata*, on lateral parts of body, temporal region, and anterior and posterior edge of tympanum in *O. lipuensis*, on eyelid and around tympanum in *O. hejiangensis*, on posterior dorsum of body and dorsal surface of hindlimbs in *O. lungshengensis*, on dorsum in *O. mawphlangensis*; tibio-tarsal articulation forward beyond the tip of snout vs. reaches the nostril in *O. anlungensis*, *O. grahami*, *O. huanggangensis*, *O. wuchuanensis* and *O. kuangwuensis*, reaches between eye and nostril in *O. schmackeri*, *O. tianmuyii*, *O. macrotympana*, reaches tip of snout or between nostril and tip of snout in *O. margaretae*, *O. swinhoana*, *O. nanjiangensis*, *O. margaretae*, *O. lungshengensis*; outer metatarsal tubercle absent vs. present in *O. swinhoana*, *O. rotodora*. The new species possesses purely black mature oocytes in life, differentiating it from *O. aureola*, *O. ishikawae*, *O. anlungensis*, *O. hejiangensis*, *O. jingdongensis*, *O. kuangwuensis*, *O. lipuensis*, *O. lungshengensis*, *O. margaretae*, *O. swinhoana*, *O. nanjiangensis*, *O. wuchuanensis*, *O. yizhangensis* (all with purely whitish yellow to yellow oocytes), *O. macrotympana* (grey oocytes), *O. andersonii*, *O. grahami*, *O. huanggangensis*, *O. junlianensis*, *O. schmackeri*, *O. tianmuyii* (their mature oocytes with dark colored animal pole and light colored vegetative pole in life). Further, the new species differs from *O. rotodora* by its snout obtusely rounded vs. obtusely pointed; upper lips brownish yellow with vertical black bars vs. light colored without bars in the latter.

Distribution and habitats. *Odorrana fengkaiensis* **sp. nov.** is a lowland dweller. At present, it was only found in three localities: Heishiding Nature Reserve (23°25'–23°30' N, 111°48'–111°55' E), located in the northern region of the Yunkai Mountains, Fengkai County, Guangdong Province; Shiwandashan Nature Reserve (21°40'–22°04' N, 107°29'–108°13' E) and Tongling Canyon (23°0'11.07"N, 106°40'2.22"E), located in the China-Vietnam border area, namely in Shangsi and Jingxi Counties, Guangxi Zhuang Autonomous Region, China. The population from Heishiding Nature Reserve inhabits broad slow-flowing mountainous streams, rivers, pools and near the riparian areas, surrounded by moist subtropical evergreen broadleaved forests at elevations between 190–510 m a.s.l. (Fig. 6); the populations from Shiwandashan Nature Reserve and Tongling Canyon inhabit around broad streams, surrounded by moist subtropical evergreen broadleaved forests or secondary limestone forests at elevations between 290–550 m a.s.l..

TABLE 3. Measurements (in mm) (minimum-maximum [mean \pm standard deviation]) of the *Odorrana fengkaiensis* sp. nov. from Heishiding Nature Reserve, Fengkai Co., Guangdong, Shiwandashan Nature Reserve, Shangsi Co. and Tongling Canyon, Jingxi Co., Guangxi; *O. hainanensis* from Hainan Island, *O. bacboensis* from Bainan Village, Napo Co., Guangxi. See materials and methods for abbreviations.

	<i>Odorrana fengkaiensis</i> sp. nov.					<i>Odorrana hainanensis</i>					<i>Odorrana bacboensis</i>	
	Males (n=11) from Fengkai, Guangdong	Females (n=22) from Fengkai, Guangdong	Females (n=9) from Shangsi and Jingxi, Guangxi	Males (n=6) from Hainan	Females (n=5) from Hainan	Male (n=1) from Napo, Guangxi	Females (n=2) from Napo, Guangxi					
SVL	37.4–51.8 (48.4 \pm 4.1)	77.3–109.9 (93.2 \pm 8.9)	89.0–111.9 (103.1 \pm 7.8)	49.1–60.7 (52.6 \pm 4.3)	94.2–120.4 (109.3 \pm 10.9)	35.6	78.0–95.0					
HDL	14.8–19.7 (18.9 \pm 1.4)	30.4–39.1 (35.4 \pm 2.4)	31.4–40.5 (36.5 \pm 3.5)	19.2–23.6 (21.1 \pm 1.6)	37.3–43.4 (40.5 \pm 2.6)	14.1	26.9–35.4					
HDW	12.4–17.3 (16.3 \pm 1.4)	36.8–36.0 (32.1 \pm 2.5)	29.8–38.4 (34.4 \pm 3.2)	16.5–20.0 (18.0 \pm 1.4)	33.9–40.6 (37.7 \pm 2.8)	11.7	23.5–32.8					
SNT	5.8–7.9 (7.2 \pm 0.5)	12.2–16.4 (14.2 \pm 1.1)	14.1–16.9 (15.4 \pm 1.1)	7.0–9.3 (7.9 \pm 0.9)	15.3–16.6 (15.9 \pm 0.5)	5.8	12.8–14.4					
IND	4.4–6.0 (5.2 \pm 0.5)	8.2–11.6 (9.8 \pm 0.9)	9.0–11.5 (10.2 \pm 0.8)	5.0–6.6 (5.7 \pm 0.6)	9.0–11.7 (10.6 \pm 1.1)	4.2	8.1–9.2					
IOD	3.3–4.3 (4.1 \pm 0.3)	6.6–11.1 (8.6 \pm 1.0)	7.6–10.4 (9.6 \pm 1.1)	3.6–4.6 (4.0 \pm 0.4)	8.5–9.8 (9.2 \pm 0.6)	2.5	7.1–7.5					
ED	5.9–8.1 (7.7 \pm 0.7)	10.0–13.5 (11.8 \pm 0.9)	10.5–12.9 (11.7 \pm 0.9)	6.4–9.6 (7.6 \pm 1.1)	10.7–12.8 (11.8 \pm 1.0)	5.2	10.1–10.4					
TYD	2.9–4.6 (4.2 \pm 0.5)	5.2–6.9 (6.0 \pm 0.5)	4.6–6.1 (5.5 \pm 0.5)	3.6–5.8 (4.5 \pm 0.9)	5.5–6.7 (6.2 \pm 0.5)	3.2	4.7–5.4					
TED	0.7–1.4 (1.2 \pm 0.2)	2.5–5.0 (3.7 \pm 0.6)	2.9–4.5 (3.8 \pm 0.4)	1.7–2.0 (1.9 \pm 0.1)	4.7–6.0 (5.2 \pm 0.5)	0.8	2.9–3.4					
HND	11.9–16.3 (15.4 \pm 1.2)	24.7–28.7 (26.8 \pm 1.2)	26.5–30.9 (28.7 \pm 1.7)	14.5–17.9 (16.1 \pm 1.2)	27.3–33.1 (29.8 \pm 2.3)	11.1	22.2–26.4					
TIB	22.9–29.7 (27.7 \pm 1.9)	46.0–58.9 (54.8 \pm 3.1)	50.0–64.8 (58.0 \pm 4.4)	28.2–35.3 (31.4 \pm 2.9)	58.9–68.6 (63.2 \pm 3.8)	22.0	45.8–52.9					
FTL	31.2–41.8 (39.2 \pm 2.8)	64.7–79.7 (74.1 \pm 3.9)	70.0–85.1 (78.0 \pm 4.9)	38.5–47.9 (42.6 \pm 3.3)	77.9–90.9 (84.5 \pm 6.1)	30.4	60.8–71.3					
FPW	0.83–1.57 (1.06 \pm 0.19)	1.87–2.86 (2.32 \pm 0.24)	2.64–3.29 (3.07 \pm 0.24)	1.8–2.1 (1.9 \pm 0.1)	3.4–3.9 (3.7 \pm 0.2)	1.25	2.5–2.9					
DPW	0.56–1.03 (0.81 \pm 0.12)	1.39–2.18 (1.72 \pm 0.19)	1.64–2.26 (2.00 \pm 0.21)	0.9–1.1 (1.0 \pm 0.1)	2.0–2.4 (2.3 \pm 0.2)	0.67	1.3–1.8					
HDL/SVL	0.37–0.41 (0.39 \pm 0.01)	0.35–0.42 (0.38 \pm 0.02)	0.33–0.37 (0.35 \pm 0.01)	0.38–0.43 (0.40 \pm 0.02)	0.36–0.40 (0.37 \pm 0.01)	0.40	0.34–0.37					
HDW/SVL	0.32–0.35 (0.34 \pm 0.01)	0.32–0.37 (0.35 \pm 0.01)	0.32–0.35 (0.33 \pm 0.01)	0.32–0.38 (0.34 \pm 0.02)	0.33–0.36 (0.35 \pm 0.01)	0.33	0.30–0.35					
HDL/HDW	1.13–1.20 (1.16 \pm 0.03)	1.04–1.16 (1.10 \pm 0.03)	1.03–1.10 (1.06 \pm 0.02)	1.13–1.20 (1.17 \pm 0.02)	1.05–1.10 (1.08 \pm 0.03)	1.21	1.08–1.14					
SNT/HDL	0.36–0.42 (0.38 \pm 0.01)	0.38–0.42 (0.40 \pm 0.01)	0.39–0.47 (0.42 \pm 0.02)	0.36–0.40 (0.38 \pm 0.02)	0.37–0.42 (0.39 \pm 0.02)	0.41	0.41–0.48					
IND/HDW	0.29–0.35 (0.32 \pm 0.02)	0.28–0.33 (0.31 \pm 0.02)	0.27–0.31 (0.30 \pm 0.01)	0.28–0.35 (0.32 \pm 0.03)	0.26–0.30 (0.28 \pm 0.01)	0.36	0.34–0.38					
IOD/HDW	0.24–0.27 (0.25 \pm 0.01)	0.25–0.31 (0.27 \pm 0.02)	0.26–0.30 (0.28 \pm 0.02)	0.21–0.23 (0.22 \pm 0.01)	0.22–0.26 (0.24 \pm 0.02)	0.21	0.23–0.30					
ED/SNT	1.01–1.16 (1.07 \pm 0.05)	0.74–0.92 (0.84 \pm 0.05)	0.69–0.82 (0.76 \pm 0.04)	0.90–1.03 (0.96 \pm 0.05)	0.69–0.79 (0.74 \pm 0.04)	0.90	0.72–0.79					
ED/HDL	0.38–0.43 (0.41 \pm 0.01)	0.30–0.38 (0.33 \pm 0.02)	0.29–0.34 (0.32 \pm 0.02)	0.33–0.41 (0.36 \pm 0.03)	0.27–0.31 (0.29 \pm 0.01)	0.37	0.29–0.38					
TED/TYD	0.24–0.33 (0.28 \pm 0.03)	0.39–0.87 (0.63 \pm 0.11)	0.58–0.88 (0.70 \pm 0.10)	0.35–0.53 (0.43 \pm 0.07)	0.74–0.95 (0.84 \pm 0.10)	0.26	0.62–0.63					
TYD/ED	0.50–0.61 (0.55 \pm 0.03)	0.43–0.58 (0.51 \pm 0.04)	0.44–0.51 (0.47 \pm 0.03)	0.55–0.68 (0.59 \pm 0.05)	0.51–0.55 (0.53 \pm 0.02)	0.62	0.47–0.52					
HND/SVL	0.30–0.35 (0.32 \pm 0.01)	0.25–0.33 (0.29 \pm 0.02)	0.26–0.30 (0.28 \pm 0.02)	0.29–0.34 (0.31 \pm 0.02)	0.26–0.29 (0.27 \pm 0.01)	0.31	0.28–0.29					
TIB/SVL	0.54–0.61 (0.57 \pm 0.03)	0.53–0.67 (0.59 \pm 0.04)	0.54–0.59 (0.56 \pm 0.02)	0.56–0.68 (0.60 \pm 0.04)	0.53–0.65 (0.58 \pm 0.04)	0.62	0.56–0.59					
FTL/SVL	0.76–0.85 (0.81 \pm 0.03)	0.72–0.88 (0.80 \pm 0.05)	0.74–0.79 (0.76 \pm 0.02)	0.77–0.87 (0.81 \pm 0.04)	0.76–0.83 (0.75 \pm 0.03)	0.85	0.75–0.78					
FPW/DPW	1.16–1.52 (1.30 \pm 0.13)	1.14–1.57 (1.35 \pm 0.11)	1.35–1.80 (1.54 \pm 0.15)	1.79–1.94 (1.87 \pm 0.06)	1.54–1.67 (1.61 \pm 0.05)	1.87	1.61–1.92					

Remarks. *O. fengkaiensis* **sp. nov.** was found on forest floor, rocks or low shrubs at night, and diving into water by disturbance. They take the shelter under submerged rocks or perhaps as entering holes in the banks during the day. All females were found on roadside and bare forest floor; all males were found on top of the bushes and scrubby branches at height of 10–30 cm, closed to adult females. The adult male individuals frequently emit a short whistling call from end of May to mid-July, and rarely emit voices for the rest of the year.

The diet and behavior of *O. fengkaiensis* **sp. nov.** remains poorly known. We dissected SYS a000174 and found seven termites in its stomach. Currently, the tadpoles and eggs of *O. fengkaiensis* have not been found in the field, showed that the reproduction behavior of this species is rather cryptic. The female individuals were commonly found in May to September, occasionally in March, April, October and November. The male juvenile was found occasionally in September. The female paratypes, including SYS a000111, SYS a00184, SYS a002161, SYS a002262 possessed mature black oocytes in oviduct. While the females, collected before May and after August, possessed under-developed oocytes in ovary. Therefore, the breeding season of this species may be during May to August.

Etymology. The specific epithet “*fengkaiensis*” refers to the locality of the holotype, Fengkai County, Guangdong Province, China. We propose the common English name “Feng-kai Odor Frog” for this species.

***Odorrana bacboensis* (Bain, Lathrop, Murphy, Orlov, & Ho, 2003), a new record for China**

Fig. 5: A

Specimens examined. Two adult female specimens SYS a001046 and SYS a001047, an adult male specimen SYS a001048 from Bainan village (23° 3'15.56" N, 105°48'57.85" E; 330 m a.s.l.), Napo County, Guangxi Zhuang Autonomous Region, China, collected by JHY and RLL on 6th august 2010.

Description of specimens from China. The head length greater than width, HDL: HDW 1.08–1.14 in females, 1.21 in male; head width 0.30–0.35 times of SVL in females, 0.33 times of SVL in male; head length 0.34–0.37 times of SVL in females, 0.40 times of SVL in male; snout short, rounded in dorsal view, bluntly rounded in profile, projecting beyond margin of lower jaw; eye large, eye diameter 0.72–0.90 times of SNT, upper eyelid wider than interorbital distance; top of head flat; canthus rostralis rounded; lip flared; loreal region concave; internasal distance larger than interorbital distance; tympanum circular, large, distinctly visible, tympanum diameter 0.47–0.52 times of eye diameter in females, 0.62 times in male; tympanum-eye distance small (TED 2.9–3.4 mm in female, 0.8 mm in male); Choanae ovoid; vomerine dentigerous processes prominent, slightly oblique, posteromedial to choanae; tongue cordiform, distinctly notched posteriorly.

Forelimbs moderately robust; hand length 0.28 times of SVL in females, 0.31 times in male; relative finger lengths II < I < IV < III; fingers free of webbing, tips of fingers dilated, becoming pointed, cordiform disks; width of disk significantly greater than width of distal phalanx of finger III, FPW:DPW = 1.61–1.92 in females, 1.87 in male; terminal phalanges T-shaped; lateroventral circummarginal grooves not meeting at the tip of disks; subarticular tubercles conical; supernumerary tubercle below the base of each finger, distinct, significantly smaller than subarticular tubercles; metacarpal tubercle three, elongated and distinct. Hindlimbs robust, relatively long; tibio-tarsal articulation beyond the tip of snout when hindlimb adpressed along the side of the body; heels overlapped when the flexed hindlimbs held at right angles to the body axis; tibia length 0.56–0.59 times of SVL in females, 0.62 times in male; feet length 0.75–0.78 times of SVL in females, 0.85 times in male; relative toe lengths I < II < III < V < IV; tips of toes dilated, becoming rounded triangular disks; circummarginal grooves present; feet fully webbed to disks, but as a fringe from distal subarticular tubercle of toe IV; slight lateral fringes on toes I and V to terminal phalanges; subarticular tubercles prominent, conical; inner metatarsal tubercle elongated, ovoid; outer metatarsal tubercle absent; inner tarsal fold absent.

Skin on dorsum shagreened with dense granules; a number of tubercles and pustules scattered on flanks of trunk; dorsolateral folds absent; supratympanic folds slightly prominent, from posterior corner of eye, curving posteroventrally, extending to a level above insertion of arm; small tubercles anterior and posterior to tympanum; venter smooth, no pectoral spinules; distinct granules present on posterior thighs and around cloaca; cloacal opening unmodified, directed posteriorly, at upper level of thighs.

Dorsum of head and body brown with reticulated green markings anterior to sacral vertebra; upper part of flank brown, lower part of flank light yellow with several large black spots; upper and lower lips creamy yellow

with vertical black bars; dorsal limbs and digits brown with black transverse bands; webbing on feet marbled white and dark brown; venter creamy white; iris golden, margin of pupil outlined in a striking reddish yellow border.

The adult female specimens SYS a001046 and 1047 possessed black mature oocytes (1.8 mm in diameter) in life; adult male specimen SYS a001048 with developed testes (size of 1.6×2.3 mm), nuptial pad on finger I, paired gular pouches at corners of throat.



FIGURE 5. Morphology and colour pattern of *Odorrana hainanensis* and *O. bacboensis* in life. **A:** SYS a001046, adult female *O. bacboensis*, from Bainan village, Napo County, Guangxi, China. **B:** adult female *O. hainanensis*, from Diaoluoshan Mountain, Hainan Island. **C:** SYS a000377, adult male *O. hainanensis*, from Diaoluoshan Mountain, Hainan Island. **D:** velvety nuptial pad on thumb in SYS a000377. Photos by Qing Du and JHY.

Variation. Measurement and body proportions of all specimens from Napo County, Guangxi are listed in Table 3. The Chinese specimens basically match with the original description of Bain *et al.* (2003), but also show morphological difference, especially in color pattern. Specifically, the dorsum of head and body decorated with reticulated green markings in Chinese specimens (lacking same green markings in original description of Bain *et al.* (2003)). In addition, head length 1.21 times of head width, 0.40 times of SVL in male SYS a001048. In contrast, Bain *et al.* (2003) reported that the head of male paratype FMNH 255611 extraordinary long, head length 1.55 times of head width, 0.51 times of SVL (SVL 54.9 mm, HDL 28.0 mm, HDW 18.1 mm). Therefore, the measurement data from the original description might be inaccurate.

Revised diagnosis. (1) SVL 35.6–54.9 mm in adult males, 78–105 mm in adult females; (2) vomerine teeth present in rows oblique to choanae; (3) vertical black stripes on lip, especially distinct under eye; (4) tympanum circular, distinct, TYD:ED 0.47–0.52 in females, 0.62–0.66 in the male; (5) supratympanic fold weak; (6) dorsal skin shagreened, becoming tubercles and pustules laterally; (7) dorsolateral fold absent; (8) venter smooth, no pectoral spinules; (9) dorsum brown with black blotches, sometimes dorsum of head and body decorated with reticulated green markings; (10) disks on fingers and toes enlarged; (11) feet fully webbed to disks, but as a fringe

from distal subarticular tubercle of IV, slight lateral fringes on toes I and V to terminal phalanges; (12) subarticular tubercles distinct, conical; (13) male with nuptial pad on finger I; (14) paired gular pouches; (15) oocytes black.

Distribution. The Chinese specimens collected from Bainan River, located in the China-Vietnam border at night, represent the first record of *O. bacboensis* for China. Furthermore, our molecular phylogenetic analyses revealed that voucher HNNU HK001, which was misidentified as *O. tiannanensis* in Chen *et al.* 2013, from Hekou County, Yunnan, China, also is classified to *O. bacboensis*. The Hekou County bordering on Vietnam, at a distance of 200 km away from Bainan Village, Napo County, Guangxi (Fig. 1). Therefore, area of occurrence of *O. bacboensis* may be significantly expanded.



FIGURE 6. Habitat of *O. fengkaiensis* sp. nov. in the type locality of Heishiding Nature Reserve, Fengkai County, Guangdong Province.

Discussion

The evolutionary species concept (Simpson 1961; Wiley 1978), where a unique single lineage of ancestor-descendent populations has its own evolutionary tendencies is commonly used in systematics and taxonomy of amphibians and reptiles (Frost & Hillis 1990). The populations from the Fengkai, Jingxi and Shangsi Counties are reciprocally monophyletic to *O. hainanensis* with a moderate level of mtDNA sequence divergence (1.9–2.4%) in our analysis although their phylogenetic relationships are unresolved. This genetic distance is low to moderate than between several other *Odorrana* species (Fig. 2), but is about the same level of the divergence separating the two sympatric species, *O. jingdongensis* and *O. andersonii*. Further studies are required to access whether such low to moderate divergence between *O. hainanensis* and *O. fengkaiensis* sp. nov. reveals a recent divergence from a common ancestral species (Li *et al.* 2009), or has been affected by historical genetic introgression (Rheindt & Edwards 2011). Sea level oscillation due to glacial-interglacial climate fluctuations is believed to occur between Hainan Island and its nearby mainland during the Quaternary period (Voris 2000). Previous studies demonstrate that these series of geological dynamics can promote either isolation or gene flow in variable animals, including insects, reptiles, birds and mammals (Chen *et al.* 2015; Huang *et al.* 2013; Lin *et al.* 2013)

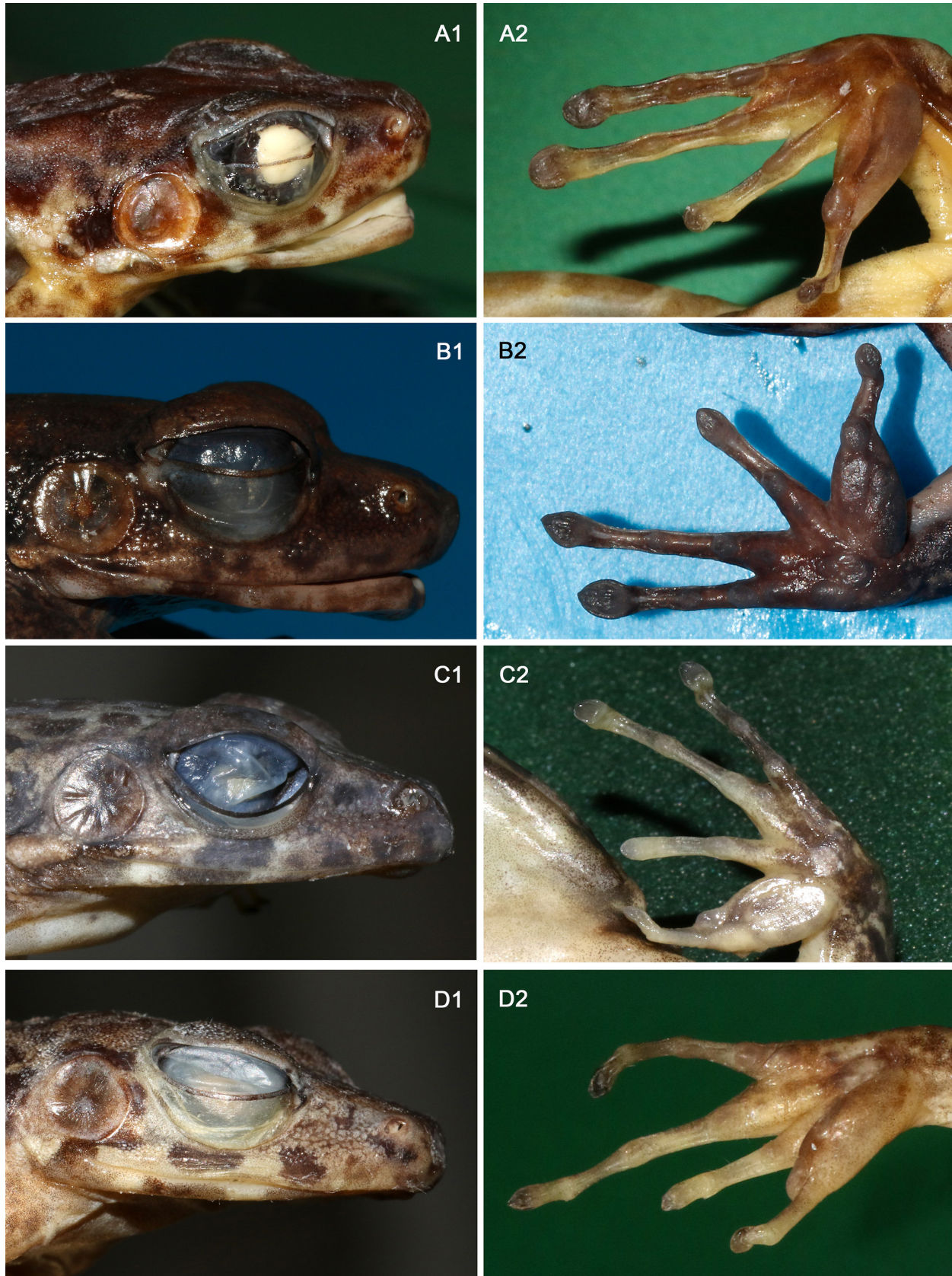


FIGURE 7. Comparisons of sister species *O. hainanensis* and *O. fengkaiensis* sp. nov. **A:** The specimen SYS a000377 of adult male *O. hainanensis*; **B:** CIB40548 of adult male *O. hainanensis*; **C:** SYS a002265 of adult male *O. fengkaiensis* sp. nov.; **D:** SYS a000176 of adult male *O. fengkaiensis* sp. nov.; **1:** showing eye, tympanum and tympanum–eye distance; **2:** showing disk width of finger III and width of distal phalanx of finger III.

Furthermore there is other evidence making us believe that they are reproductive isolation. First, the insular taxa *O. hainanensis* is obviously isolated from the proposed new species with geographical barrier. Second, *O. fengkaiensis* **sp. nov.** is an inland mountainous dweller, bearing pure black oocytes in oviducts and *hainanensis* is an insular species, bearing oocytes with blackish brown animal pole and yellowish white vegetative pole (Fei *et al.* 2001). This differentiation might reflect possible breeding habits in Cascade ranids: in general, species lay melanic oocytes in sun-exposed habitat to promote egg development (Pope 1931) and species lays white or pigmentless oocytes in habitats that are shaded from the sunlight (Duellman & Trueb 1986). Therefore, we believe this might cast consistent differences in traits, correlated with local adaptation and thus different evolutionary tendency. Overall, our study shows that the taxon of genus *Odorrana* from the Fengkai County, Guangdong, Shangsi and Jingxi Counties, Guangxi, China, represents a distinct species status, which is described above as a new species, *Odorrana fengkaiensis* **sp. nov.**. Future research should focus on the distribution of the new species and its life history.

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APPENDIX I. List of specimens examined in this study.

- Odorrana hainanensis* (14): China: Hainan Province: Mt. Wuzhishan: CIB 40547–40550; Diaoluoshan Nature Reserve: CIB 40551–556, SYS a000377, 0636, 0703, 2260.
- Odorrana jingdongensis* (1): China: Yunnan Province: Zhenyuan County, Ailaoshan Nature Reserve: SYS a002995.
- Odorrana huanggangensis* (21): China: Fujian Province: Sangang Village: SYS a001724 and 1725; Jiangle County: Longqishan Nature Reserve: SYS a002502 and 2503. Jiangxi Province: Yanshan County: Wuyishan Nature Reserve: SYS a001327, 1328, 1329, 1344 and 1345; Guixi City: Yangjifeng Nature Reserve: SYS a000237, 0380 and 0381; Guangfeng County: Tongboshan Nature Reserve: SYS a001689, 1690, 1691, 1692 and 1693; Guangdong Province: Ruyuan County: Naling Nature Reserve: SYS a000504, 0505, 0827 and 2121.
- Odorrana lungshengensis* (4): China: Guizhou Province: Leishan County: Leigongshan Nature Reserve: SYS a002229, 2230 and 2231. Guangxi Zhuang Autonomous Region: Xing'an County: Mao'ershan Nature Reserve: SYS a002290.
- Odorrana margaretae* (9): China: Hubei Province: Jianshi County: Chayuangou Village: SYS a002317, 2318, 2323, 2324, 2325. Sichuan Province: Mt. Emei: SYS a001791, 1792, 1793 and 1794.
- Odorrana schmackeri* (2): China: Hubei Province: Jianshi County: Chayuangou Village: SYS a002319, 2322.
- Odorrana tianmuisi* (7): China: Zhejiang Province: Lin'an City: Mt. Tianmu: SYS a002680, 2681, 2682 and 2683. Anhui Province: Huangshan City: Fucun Village: SYS a002696, 2697 and 2698.
- Odorrana wuchuanensis* (2): China: Hubei Province: Jianshi County: Chayuangou Village: SYS a002315, 2321.
- Odorrana yizhangensis* (12): China: Guangdong Province: Ruyuan County: Naling Nature Reserve: SYS a000594, 0595, 0596, 0597, 0598 and 0704. Jiangxi Province: Mt. Jinggang: SYS a001109, 1110, 1869 and 1870. Hunan Province: Yanling County: Taoyuandong Nature Reserve: SYS a001847 and 1848.