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A New Species of Odorous Frog Genus *Odorrana* (Anura, Ranidae) from Southern Guizhou Province, China

Tao LUO[1#], Siwei WANG[2#], Ning XIAO[3#], Yali WANG[2] and Jiang ZHOU[1*]

[1] *School of Karst Science, Guizhou Normal University, Guiyang 550001, Guizhou, China*
[2] *School of Life Sciences, Guizhou Normal University, Guiyang 550001, Guizhou, China*
[3] *Guiyang Nursing Vocational College, Guiyang 550003, Guizhou, China*

Abstract We describe *Odorrana liboensis* **sp. nov.**, a new species from the Maolan National Nature Reserve, Libo County, Guizhou Province, China. Phylogenetic analyses based on DNA sequences of the mitochondrial 12S rRNA, 16S rRNA, and ND2 genes supported the new species as an independent lineage, closely related to *O. lipuensis*. The uncorrected genetic distances between the 12S rRNA and 16S rRNA in the new species and its closest congener, *O. lipuensis*, were 6.06% and 5.19%, respectively. The new species is distinguished from its congeners by a combination of the following morphological characters: (1) having medium body size, with the snout-vent length (SVL) of adult females approximately 1.2 times as long as males at 56.9 ± 1.0 (55.8–58.2 mm, n = 9) in females and 48.7 ± 1.2 (47.1–49.9 mm, n = 5) in males; (2) head length greater than width in males and females; (3) tympanum distinctly visible, greater than one-half the diameter of the eye; (4) eyes big and prominent, width of upper eyelid (UEW) approximately 3/4 of eye diameter (ED); (5) dorsolateral folds absent; (6) two metacarpal tubercles; (7) relative finger lengths: II < I < IV < III; (8) subarticular tubercles on fingers prominent: 1, 1, 2, 2; (9) one metatarsal tubercle; (10) tibiotarsal articulation reaching to between the eye and nostril when the leg is stretched forward; (11) toes with entire webbing to disks; (12) subarticular tubercles on toes prominent: 1, 1, 2, 3, 2; (13) dorsal surfaces of limbs with distinct brownish-black bands; (14) smooth, grass-green dorsum with irregular brown mottling; (15) venter smooth, lacking black spots; and (16) lacking pectoral spinules, lacking vocal sacs, and light white nuptial pad present on finger I in males. The new species is currently only known from the type locality.

Keywords Taxonomy, morphology, *Odorrana*, *Odorrana liboensis* **sp. nov.**, karst cave, Guizhou

1. Introduction

The genus *Odorrana* was first recognized by Fei *et al.* (1990) with the type species *Odorrana margaretae* (Liu, 1950). Despite previous controversy over classification (Dubois, 1992; Matsui, 1994), molecular phylogenetic analyses suggested that *Odorrana* forms a well-supported monophyletic group (Matsui *et al.*, 2005; Ngo *et al.*, 2006; Cai *et al.*, 2007; Che *et al.*, 2007; Stuart, 2008; Chen *et al.*, 2013; Li *et al.*, 2018a). According to Frost (2021), *Odorrana* contains at least 61 recognized species and is widely distributed in montane streams and rivers in the subtropical and tropical regions of East and Southeast Asia (Fei *et al.*, 2012; AmphibiaChina, 2021; Frost, 2021). The range of species in this genus covers the Ryukyu Archipelago, southern China, northeastern India, and the Thai-Malay Peninsula, and extends southwards to Sumatra and Borneo (Frost, 2021). All species in the genus are associated with mountain streams except for *O. wuchuanensis* (Xu, 1983) and *O. lipuensis* Mo, Chen, Wu, Zhang & Zhou, 2015, which occur in dark caves.

Among the *Odorrana* species, 39 occur in China and 24 of these are endemic to China (Fei *et al.*, 2012; AmphibiaChina, 2021; Frost, 2021; Chen *et al.*, 2020; Shen *et al.*, 2020; Liu *et al.*, 2021). Fei *et al.* (1990) established *Odorrana*, and later Ye and Fei (2001) suggested four species groups (*O. andersonii*,

[#]These authors contributed equally to this paper
[*] Corresponding authors: Dr. Jiang ZHOU, from Guizhou Normal University, China, with his research focusing on zoology.
E-mail: zhoujiang@ioz.ac.cn
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O. kuangwuensis, *O. schmacheri*, and *O. livida*) within *Odorrana* based on a morphological phylogenetic study. Fei *et al.* (2005) established two subgenera (*Odorrana* and *Bamburana*) within *Odorrana* and recognized *Odorrana versabilis* as the type species of *Bamburana*. Molecular phylogenetic studies support the division of species groups within *Odorrana* but not the two subgenera (Che *et al.*, 2007). Subsequently, Fei *et al.* (2009) divided the Chinese *Odorrana* species into six species groups (*O. tormota*, *O. taiwaniana*, *O. graminea*, *O. margaretae*, *O. schmackeri*, and *O. andersonii*; *O. taiwaniana* is a synonym for *O. swinhoana*) based on morphological characters. These divisions have been accepted by other researchers and applied to the *Odorrana* species distributed outside China (Pham *et al.*, 2016; Li *et al.*, 2018a). However, recent studies have rejected the monophyly of the *O. margaretae*, *O. schmackeri*, and *O. andersonii* species groups (Chen *et al.*, 2013). The phylogenetic relationships between these species groups, the species included in the species groups, and the species group affiliations of new species published in recent years are unclear.

The montane river and stream habitats of most *Odorrana* may promote intraspecific divergence through geographical isolation, especially given the wide geographical range of the complex (Chen *et al.*, 2013; Li *et al.*, 2015). Indeed, many cryptic species of *Odorrana* have been discovered. For example, 25 new species of *Odorrana* have been described since 2005 (See species list of the genus *Odorrana* in Frost (2021) and AmphibiaChina (2021)). This indicates that further discoveries or potential taxonomic changes within *Odorrana* are likely.

From 2016 to 2018, 14 specimens of an unknown species of *Odorrana* were collected inside a completely dark karst cave in the Maolan National Nature Reserve, Libo County, Guizhou Province, China. Morphologically, these specimens most closely resemble *O. lipuensis* and *O. kweichowensis* Li, Xu, Lv, Jiang, Wei & Wang, 2018 (Mo *et al.*, 2015; Li *et al.*, 2018a), but differ from *O. lipuensis*, *O. kweichowensis*, and all other *Odorrana* from China and adjoining countries. They inhabit a dark karst cave environment similar to that of *O. wuchuanensis* and *O. lipuensis* but are morphologically very different from *O. wuchuanensis* and *O. lipuensis*. To distinguish these specimens, we conducted phylogenetic analyses based on mitochondrial DNA and morphological comparisons. All of the analyses consistently indicated that the specimens from Maolan National Nature Reserve are a new taxon. We describe this taxon here as a new species.

2. Materials and Methods

2.1. Sampling A total of 72 specimens were collected in this study. Fourteen specimens were of the undescribed species from Maolan National Nature Reserve in Libo County, Guizhou Province; 35 were *O. kweichowensis* from Lengshuihe Nature Reserve in Jinsha County, Guizhou Province; four were *O. yizhangensis* Fei, Ye & Jiang, 2007 from Kuankoushui National Nature Reserve in Suiyang County, Guizhou Province, and Yuntai Mountain, Shibing County; one was *O. huanggangensis* Chen, Zhou & Zheng, 2010 from Yueliangshan Nature Reserve in Conjiang County, Guizhou Province; one was *O. kweichowensis* from Maolan National Nature Reserve in Libo County, Guizhou Province; and 17 were *O. wuchuanensis* from Maolan National Nature Reserve, Libo County, Guizhou Province (Figure 1). All of the specimens were fixed in 10% buffered formalin and later transferred to 75% ethanol for preservation. The muscles used for molecular analysis were preserved in 95% alcohol at –20 °C. All of the specimens were deposited in Guizhou Normal University (GZNU), Guiyang City, Guizhou Province, China.

2.2. DNA Extraction, PCR amplification, and sequencing Genomic DNA was extracted from muscular tissue using a DNA extraction kit from Tiangen Biotech Co., Ltd. (Beijing). All samples were sequenced for three mitochondrial genes: partial 12S ribosomal RNA gene (12S rRNA), 16S ribosomal RNA gene (16S rRNA), and NADH dehydrogenase subunit 2 (ND2). The primers used for 12S rRNA were 12SF (5'-GGTTTGRTCCTRGCCTTAC-3') and 12SR (5'-CCATGTTACGACTTGCCTCT-3') following Chen *et al.* (2013), the primers used for 16S rRNA were 16SF (5'-ACGAGCCTAGTGATAGCTGGTT-3') and 16SR (5'-CGGTCTGAACTCAGATCACGT-3') following Chen *et al.* (2013), and the primers used for ND2 were Gln-LND2 (5'-CCCTTTGCACTTCCTTTATGC-3') and Ala-HND2 (5'-GGCCTGAGTTGCATTCATG-3') following Li *et al.* (2015). PCR amplifications were performed in a 25 μL reaction volume with the following cycling conditions: an initial denaturing step at 95 °C for five min; 36 cycles of denaturing at 95 °C for 40 s, annealing at 52 °C (for 12S rRNA)/49 °C (for 16S rRNA)/60 °C (for ND2) for 40 s and extending at 72 °C for 1 min, and a final extending step of 72 °C for 10 min. The PCR products were sequenced on an ABI Prism 3730 automated DNA sequencer in Chengdu TSING KE Biological Technology Co. Ltd. (Chengdu, China). All of the sequences have been deposited in GenBank (Table 1). Some homologous DNA sequences of voucher specimens of related species were downloaded from GenBank and incorporated into the phylogenetic analyses.

2.3. Phylogenetic analyses We used a total of 187 sequences (including 72 12S rRNA, 79 16S rRNA, and 36 ND2 gene sequences) for molecular analyses. Three mitochondrial genes from 11 muscle tissues were sequenced and 154 sequences downloaded from GenBank from 48 species of the genus *Odorrana* were used. These included the undescribed species

from China that was named in this study (Figure 1). A total of 26 sequences were downloaded from GenBank as out-groups (Chen *et al.*, 2013). Detailed information on these materials is shown in Table 1.

All of the sequences were assembled and aligned using the MUSCLE (Edgar, 2004) module in MEGA 7.0 (Kumar *et al.*, 2016) with default settings. Alignments were checked by eye and revised manually if necessary. Trimming with the gaps partially deleted was performed in GBLOCKS 0.91b (Castresana, 2000). Phylogenetic trees were constructed with both maximum likelihood (ML) and Bayesian inference (BI). The ML was conducted in IQ-TREE (Nguyen *et al.*, 2015) with 2000 ultrafast bootstrapping (Hoang *et al.*, 2018) and was performed until a correlation coefficient of at least 0.99 was reached. The BI was performed in MrBayes 3.2.1 (Ronquist *et al.*, 2012), and the best-fit model was obtained by the Bayesian inference criteria (BIC) computed with PartitionFinder 2 (Lanfear *et al.*, 2016). For this analysis, 12S rRNA, 16S rRNA, and ND2 genes were defined.

The analysis suggested that the best partition scheme was 12S rRNA/16S rRNA/ND2 genes. We selected GTR+I+G as the best model for 12S rRNA and 16S rRNA and the TIM+I+G model as the best model for the ND2 gene. Two independent runs were conducted in BI analysis, each of which was performed for 2,000,000 generations and sampled every 1000 generations. The first 25% of the samples were discarded as burn-in, resulting in a potential scale reduction factor (PSRF) of <0.01. Nodes in the trees were considered well supported when Bayesian posterior probabilities (BPP) were ≥0.95 and the ML ultrafast bootstrap value (UFB) was ≥95%. Uncorrected *p*-distances (1000 replicates) based on 12S rRNA and 16S rRNA were calculated in MEGA 7.0 (Kumar *et al.*, 2016).

2.4. Morphological analysis Morphometric data were taken from 74 well-preserved adult specimens (voucher information in Table 2 and Table S1). Measurements were recorded to the nearest 0.1 mm with digital calipers by Tao

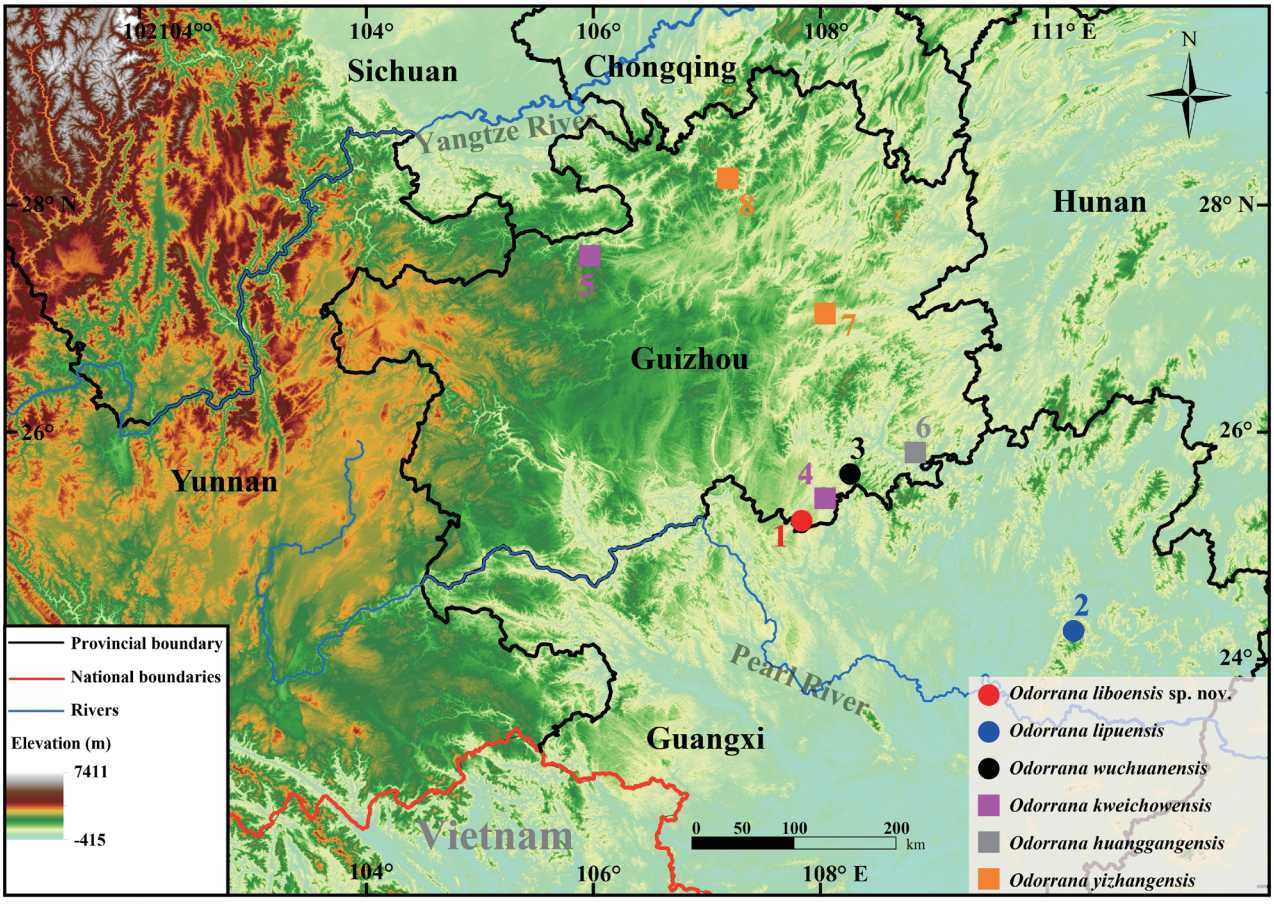

Figure 1 Sampling collection localities and distribution of the *Odorrana liboensis* sp. nov., *O. lipuensis*, *O. wuchuanensis*, *O. kweichowensis*, *O. huanggangensis*, and *O. yizhangensis* in southwest China. 1. Maolan National Nature Reserve, Libo County, Guizhou, China. 2. Lipu County, Guangxi, China. 3. Jiarong Town, Libo County, Guizhou, China. 4. Maolan National Nature Reserve, Libo County, Guizhou, China. 5. Lengshuihe Nature Reserve, Jinsha County, Guizhou, China. 6. Yueliangshan Nature Reserve, Congjiang County, Guizhou, China. 7. Yuntai Mountains, Shibing County, Guizhou, China. 8. Kuankuoshui National Nature Reserve, Suiyang County, Guizhou, China. The base maps are from Standard Map Service website (http://bzdt.ch.mnr.gov.cn/index.html).

Table 1 Localities, voucher information, and GenBank numbers for all samples used in this study.

ID	Species	Locality	Voucher	12S	16S	ND2
1	*Odorrana nasuta*	Wuzhishan City, Hainan, China	HNNU051119	KF185017	KF185053	-
2	*Odorrana versabilis*	Leigongshan Nature Reserve, Leishan County, Guizhou, China	HNNU003	KF185019	KF185055	-
3	*Odorrana exiliversabilis*	Wuyishan City, Fujian, China	HNNU0607032	KF185020	KF185056	-
4	*Odorrana nasica*	HaTinh, Vietnam	AMNH A161169	DQ283345	DQ283345	-
5	*Odorrana yentuensis*	Guangxi, China	NHMG1401035	MH665669	MH665675	-
6	*Odorrana tormota*	Huangshan City, Anhui, China	No. AM04005	DQ835616	DQ835616	DQ835616
7	*Odorrana amamiensis*	Tokunoshima, Ryukyu	KUHE:24635	AB200923	AB200947	AB600991
8	*Odorrana narina*	Okinawa Island, Japan	-	AB511287	AB511287	AB600990
9	*Odorrana supranarina*	Iriomotejima, Ryukyu	KUHE:12898	AB200926	AB200950	-
10	*Odorrana swinhoana*	Nantou County, Taiwan, China	HNNUTW9	KF185010	KF185046	-
11	*Odorrana utsunomiyaorum*	Iriomotejima, Ryukyu	KUHE:12896	AB200928	AB200952	-
12	*Odorrana aureola*	Phu Rua District, Loei Prov., Thailand	FMNH 265919	-	DQ650564	DQ650500
13	*Odorrana livida*	Prachuap Kirikhan Prov., Thailand	FMNH 263415	KF771294	DQ650613	DQ650546
14	*Odorrana leporipes*	Shaoguan City, Guangdong, China	HNNU1008I099	KF185000	KF185036	-
15	*Odorrana chloronota*	Ha Giang, Vietnam	AMNH A163935	DQ283394	DQ283394	-
16	*Odorrana graminea*	Wuzhishan City, Hainan, China	HNNU0606123	KF185002	KF185038	-
17	*Odorrana hosii*	Kuala Lumpur, Malaysia	IABHU 21004	AB511284	AB511284	-
18	*Odorrana banaorum*	Tram Lap, Vietnam	ROM 7472	AF206106	AF206487	-
19	*Odorrana morafkai*	TramLap, Vietnam	ROM 7446	AF206103	AF206484	-
20	*Odorrana kweichowensis*	Maolan National Nature Reserve, Libo County, Guizhou, China	GZNU20170725018	MW481349	MW481360	MW481371
21	*Odorrana kweichowensis*	Lengshuihe Nature Reserve, Jinsha County, Guizhou, China	CIBjs20171014001	MH193539	MH193551	MH193605
22	*Odorrana schmackeri*	Yichang City, Hubei, China	HNNU0908II349	KF185011	KF185047	-
23	*Odorrana schmackeri*	Badagongshan Nature Reserve, Sangzhi County, Hunan, China	CIB20130531	MH193543	MH193555	MH193609
24	*Odorrana bacboensis*	Khe Moi, Nghe An, Vietnam	ROM 13044	AF206099	AF206480	DQ650505
25	*Odorrana tiannanensis*	Hekou County, Yunnan, China	HNNUHK001	KF185008	KF185044	-
26	*Odorrana fengkaiensis*	Heishiding Nature Reserve, Fengkai County, Guangdong, China	SYS a002262	KT315354	KT315375	-
27	*Odorrana hainanensis*	Wuzhishan City, Hainan, China	HNNU0606105	KF184996	KF185032	-
28	*Odorrana nanjiangensis*	Yichang County, Hubei, China	HNNU1007I061	KF185005	KF185041	-
29	*Odorrana hejiangensis*	Hejiang County, Sichuan, China	HNNU1007I202	KF185016	KF185052	-
30	*Odorrana huanggangensis*	Yueliangshan Nature Reserve, Congjiang County, Guizhou, China	GZNU20170822001	MW481348	MW481359	MW481370
31	*Odorrana huanggangensis*	Fanjingshan Nature Reserve, Jiangkou County, Guizhou, China	CIBFJS20150502002	MH193532	MH193565	MH193614
32	*Odorrana huanggangensis*	Wuyishan Nature Reserve, Fujian, China	HNNU0607001	KF185023	KF185059	-
33	*Odorrana tianmuii*	Lin'an area , Zhejiang , China	HNNU707071	KF185004	KF185040	-
34	*Odorrana grahami*	Kunming City, Yunnan, China	HNNU1008II016	KF185015	KF185051	-
35	*Odorrana junlianensis*	Junlian, Sichuan, China	HNNU002JL	KF185022	KF185058	-
36	*Odorrana andersonii*	Longchuan County, Yunnan, China	HNNU001YN	KF185021	KF185057	-
37	*Odorrana kuangwuensis*	Nanjiang County, Sichuan, China	HNNU0908II185	KF184998	KF185034	-
38	*Odorrana margaretae*	Emei City, Sichuan, China	HNNU20050032	KF184999	KF185035	-
39	*Odorrana jingdongensis*	Jingdong County, Yunnan, China	20070711017	KF185014	KF185050	-
40	*Odorrana daorum*	Sa Pa, Vietnam	ROM 19053	AF206101	AF206482	-
41	*Odorrana hmongorum*	Lao Cai, Vietnam	ROM 38605 paratype	-	EU861556	EU861585
42	*Odorrana wuchuanensis*	Maolan National Nature Reserve, Libo County, Guizhou, China	GZNU20180608018	MW481342	MW481353	MW481364
43	*Odorrana wuchuanensis*	Maolan National Nature Reserve, Libo County, Guizhou, China	GZNU20180608019	MW481343	MW481354	MW481365
44	*Odorrana wuchuanensis*	Wuchuan County, Guizhou, China	HNNU019L	KF185007	KF185043	-
45	*Odorrana mutschmanni*	Cao Bang , Vietnam	IEBR 3725	KU356762	KU356766	-
46	*Odorrana yizhangensis*	Kuankuoshui National Nature Reserve, Suiyang County, Guizhou, China	GZNU2018060802	MW481344	MW481355	MW481366
47	*Odorrana yizhangensis*	Kuankuoshui National Nature Reserve, Suiyang County, Guizhou, China	GZNU20180608011	MW481345	MW481356	MW481367
48	*Odorrana yizhangensis*	Kuankuoshui National Nature Reserve, Suiyang County, Guizhou, China	GZNU20180608012	MW481346	MW481357	MW481368
49	*Odorrana yizhangensis*	Yuntai Mountain, Shibing County, Guizhou, China	GZNU20170718002	MW481347	MW481358	MW481369
50	*Odorrana yizhangensis*	Nanling Nature Reserve, Ruyuan County, Guangdong, China	CIBHN201108149	MH193540	MH193560	MH193615
51	*Odorrana yizhangensis*	Nanling Nature Reserve, Ruyuan County, Guangdong, China	HNNU1008I075	KF185012	KF185048	-
52	*Odorrana lungshengensis*	Leigongshan Nature Reserve, Leishan County, Guizhou, China	CIBLS20140616004	MH193533	MH193553	MH193607
53	*Odorrana lungshengensis*	Longsheng County, Guangxi, China	HNNU70028	KF185018	KF185054	-
54	*Odorrana anlungensis*	Anlong County, Guizhou, China	HNNU1008I109	KF185013	KF185049	-
55	*Odorrana chapaensis*	Lai Chau, Vietnam	AMNH A161439	DQ283372	DQ283372	-
56	*Odorrana geminata*	Ha Giang, Vietnam	AMNH 163782	-	EU861546	EU861572
57	*Odorrana ishikawae*	Amami Island, Japan	IABHU 5275	AB511282	AB511282	AB511282
58	*Odorrana absita*	Xe Kong, Laos	FMNH 258107	-	EU861542	EU861568
59	*Odorrana lipuensis*	Lipu County, Guangxi, China	NHMG1303018	MH665670	MH665676	-
60	*Odorrana lipuensis*	Lipu County, Guangxi, China	NHMG1303019	-	KM388701	-
61	*Odorrana lipuensis*	Lung Tung Village, Ha Lang , Cao Bang , Vietnam	IEBR:A2015_63	-	LC155910	-
62	*Odorrana lipuensis*	Coong Village, Ha Lang , Cao Bang, Vietnam	IEBR:A2015_65	-	LC155911	-
63	*Odorrana liboensis* **sp. nov.**	Maolan National Nature Reserve, Libo County, Guizhou, China	GZNU20180608007	MW481339	MW481350	MW481361
64	*Odorrana liboensis* **sp. nov.**	Maolan National Nature Reserve, Libo County, Guizhou, China	GZNU20180608009	MW481340	MW481351	MW481362
65	*Odorrana liboensis* **sp. nov.**	Maolan National Nature Reserve, Libo County, Guizhou, China	GZNU20160802003	MW481341	MW481352	MW481363
66	*Amolops loloensis*	Shimian County, Sichuan, China	SM-ZDTW-01	NC_029250	NC_029250	NC_029250
67	*Amolops mantzorum*	Xiling Snow Mountain, Dayi County, Sichuan, China	-	NC_024180	NC_024180	NC_024180
68	*Amolops granulosus*	Wawushan Mountain, Sichuan, China	20130258	NC_044901	NC_044901	NC_044901
69	*Amolops* sp.	Gai Lai, Vietnam	-	KU840519	KU840606	-
70	*Amolops ricketti*	Wugongshan Mountain, Jiangxi, China	AM13988	NC_023949	NC_023949	NC_023949
71	*Amolops wuyiensis*	-	-	NC_025591	NC_025591	NC_025591
72	*Amolops hongkongensis*	Wuyishan, Fujian , China	DYTW-WYS-001	KX233864	KX233864	KX233864
73	*Hylarana guentheri*	Fuzhou City, Fujian, China	SCUM-H002CJ	KX269219	KX269219	-
74	*Hylarana spinulosa*	Wuzhishan City, Hainan, China	HNNU051117	KF185031	KF185067	-
75	*Glandirana tientaiensis*	Huangshan, Anhui, China	SCUM0405192CJ	KX269222	KX269222	KX269435
76	*Pelophylax nigromaculata*	Hongya, Sichuan, China	SCUM045199CJ	KX269216	KX269216	KX269431
77	*Babina adenopleura*	-	A-A-WZ001	NC_018771	NC_018771	NC_018771
78	*Babina daunchina*	Emeishan City, Sichuan, China	HNNU20060103	KF185029	KF185065	-
79	*Rana weiningensis*	Weining County, Guizhou, China	SCUM0405171	KX269217	KX269217	KX269432

Table 2 Measurements of the adult specimens of *Odorrana liboensis* **sp. nov**. and *Odorrana lipuensis*. All units are in mm. See abbreviations for the morphological characters in the Materials and Methods section. (M=male, F=female, other abbreviations defined in text).

Species	Sex	Voucher	SVL	HDL	HDW	SL	IND	NED	NSD	IOD	IFE	IAE	UEW	ED	TD	LAHL	LAN	HAL	HLL	TL	TW	TFL	FOL	TED	FD3	DPW3
Odorrana liboensis **sp. nov.**	M	GZNU 20180608002	47.1	17.3	14.9	6.5	5.0	3.8	2.8	4.8	9.4	14.3	4.3	5.2	3.6	21.7	4.6	12.8	102.3	27.7	6.4	35.4	26.0	2.0	2.5	2.5
Odorrana liboensis **sp. nov.**	M	GZNU 20180608003	48.3	18.2	14.7	8.2	5.6	3.2	3.1	4.6	9.3	14.3	3.9	6.4	3.2	20.5	4.7	12.7	102.7	26.4	6.9	38.7	26.8	2.1	2.3	2.6
Odorrana liboensis **sp. nov.**	M	GZNU 20180608004	49.8	17.6	15.6	7.2	5.1	4.5	2.9	5.6	9.2	14.6	4.8	4.7	3.5	20.9	3.5	11.2	92.5	30.2	6.9	38.6	26.4	2.2	2.4	2.7
Odorrana liboensis **sp. nov.**	M	GZNU 20180608006	49.9	17.5	15.5	7.0	5.2	3.7	3.3	6.3	9.1	14.7	3.9	5.4	3.4	20.8	3.0	12.5	92.8	31.1	6.6	38.5	26.8	2.1	2.1	2.6
Odorrana liboensis **sp. nov.**	M	GZNU 20180608007	48.9	17.1	14.0	7.4	5.1	4.0	3.4	6.5	8.3	14.6	4.6	5.4	3.3	21.0	3.1	12.6	88.2	34.2	6.8	36.4	25.8	2.2	2.2	2.5
Odorrana liboensis **sp. nov.**	M	GZNU 20180608009	49.7	16.9	15.0	7.5	5.4	4.2	3.2	6.3	9.6	14.4	4.2	5.6	3.1	22.6	3.7	12.2	90.4	32.4	6.5	36.8	26.5	2.1	2.1	2.7
Odorrana liboensis **sp. nov.**	M	GZNU 20180608010	49.5	16.7	13.8	6.7	4.8	3.1	3.6	6.5	9.5	14.8	3.5	5.5	3.8	21.4	3.6	12.7	86.8	35.8	6.4	36.8	24.5	1.9	2.4	2.8
Odorrana liboensis **sp. nov.**	M	GZNU 20180608011	47.5	18.4	15.4	7.2	5.3	3.2	4.0	6.8	9.4	15.3	3.5	5.9	3.7	21.1	3.4	12.6	88.5	30.8	6.3	36.6	25.7	2.1	2.5	2.6
Odorrana liboensis **sp. nov.**	M	GZNU 20180608012	47.2	18.1	15.5	7.9	5.5	4.0	4.0	6.4	9.5	15.1	4.2	6.5	3.7	20.8	3.5	12.2	90.5	27.4	6.9	38.1	26.9	2.1	2.4	2.7
Odorrana liboensis **sp. nov.**	F	GZNU 20180815001	56.2	20.7	18.6	8.9	5.3	5.2	2.7	7.2	10.2	15.4	4.4	6.5	4.8	28.2	3.5	12.1	102.7	31.1	6.3	42.2	27.2	2.1	2.6	2.2
Odorrana liboensis **sp. nov.**	F	GZNU 20160802001	55.8	20.9	18.9	8.5	6.8	6.6	3.2	7.4	11.1	17.3	4.8	6.5	5.9	29.7	4.3	14.4	105.3	41.5	7.6	48.5	31.3	3.4	3.0	2.5
Odorrana liboensis **sp. nov.**	F	GZNU 20160802002	56.8	20.9	18.2	8.8	5.5	5.8	2.9	7.3	10.7	15.8	4.7	6.6	4.9	28.7	3.8	12.3	103.8	32.5	6.8	42.5	27.6	2.4	2.7	2.3
Odorrana liboensis **sp. nov.**	F	GZNU 20160802003	58.2	21.5	19.5	9.1	6.6	6.2	3.3	7.9	12.2	16.5	5.1	6.9	5.1	28.5	4.2	12.9	111.5	39.9	7.3	44.6	29.9	3.1	3.1	2.8
Odorrana liboensis **sp. nov.**	F	GZNU 20160729009	57.6	19.3	19.1	9.5	6.3	5.9	3.2	7.6	11.6	15.2	4.9	5.5	4.9	29.7	5.1	14.1	110.6	36.3	6.8	43.2	28.3	2.5	2.5	2.2
Odorrana lipuensis	M	NHMG 1306001	47.7	15.6	14.6	6.5	4.4	4.3	3.1	3.7	8.3	10.4	4.0	5.5	4.1	22.4	4.7	12.8	74.6	24.1	5.6	33.8	23.0	1.3	1.7	1.5
Odorrana lipuensis	M	NHMG 1306002	40.7	14.8	13.6	6.6	4.2	3.6	3.2	3.2	7.1	10.3	3.7	4.3	3.4	20.1	5.0	11.6	68.2	24.5	5.0	30.9	20.9	1.5	2.0	1.6
Odorrana lipuensis	M	NHMG 20140702	42.5	15.1	13.2	5.7	3.6	3.5	2.7	4.1	6.8	9.9	3.2	4.3	3.5	17.8	3.7	11.5	72.8	21.6	4.7	31.1	21.7	1.3	1.5	1.2
Odorrana lipuensis	M	NHMG 20140703	41.6	14.6	13.3	5.6	4.5	3.5	2.2	3.9	7.8	11.4	3.6	4.8	3.2	18.4	3.9	10.3	76.9	22.9	3.9	31.4	19.5	1.4	1.2	1.1
Odorrana lipuensis	F	NHMG 1303019	54.1	19.7	20.5	8.2	5.5	4.6	3.5	4.8	9.5	14.9	5.1	5.9	5.1	27.8	3.2	15.8	93.1	27.5	4.7	37.8	26.8	2.2	2.6	2.1
Odorrana lipuensis	F	NHMG 1303018	49.9	17.9	17.3	7.9	4.5	5.2	2.9	4.9	8.5	13.7	4.9	5.9	4.1	26.5	3.3	14.3	96.8	26.5	4.6	26.1	25.4	1.9	2.3	1.8
Odorrana lipuensis	F	NHMG 20140701	52.1	17.2	17.3	8.2	5.2	4.6	3.1	4.7	9.2	12.9	4.7	5.1	3.8	25.6	3.4	14.1	95.0	28.9	5.1	38.6	26.7	1.8	1.7	1.7
Odorrana lipuensis	F	NHMG 1306003	52.8	19.4	18.1	8.2	4.7	4.7	3.7	5.6	8.8	14.6	5.2	6.5	4.5	26.2	4.8	14.6	93.3	27.8	6.6	37.6	26.1	2.3	1.9	2.3

Note: The morphological data of *Odorrana lipuensis* were obtained from measurements of specimen 8 by Tao LUO and Siwei WANG at the Guangxi Nature Museum.

Luo following Fei *et al*. (2009) and Li *et al*. (2018a). A total of 24 morphological characteristics were measured. These measurements were as follows: **SVL**=snout-vent length (distance from the tip of the snout to the posterior edge of the vent), **HDL**=head length (distance from the tip of the snout to the articulation of jaw), **HDW**=maximum head width (greatest width between the left and right articulations of jaw), **SL**=snout length (distance from the tip of the snout to the anterior corner of the eye), **IND**=internasal distance (minimum distance between the inner margins of the external nares), **NED**=nasal to eye distance (distance between the nasal and the anterior corner of the eye), **NSD**=nasal to snout distance (distance between the nasal the posterior edge of the vent), **IOD**=interorbital distance (minimum distance between the inner edges of the upper eyelids), **IFE**=distance between anterior corner of eye, **IAE**=distance between posterior corner of eyes, **UEW**=upper eyelid width (greatest width of the upper eyelid margins measured perpendicular to the anterior-posterior axis), **ED**=eye diameter (distance from the anterior corner to the posterior corner of the eye), **TD**=tympanum diameter, **LAHL**=length of lower arm and hand (distance from the elbow to the distal end of the finger IV), **LAN**=width of lower arm, **HAL**=hand length (distance from the posterior end of the inner metacarpal tubercle to the distal tip of Finger IV), **HLL**=hindlimb length (maximum length from the vent to the distal tip of the toe IV), **TL**=tibia length (distance from knee to tarsus), **TW**=maximal tibia width, **TFL**=length of foot and tarsus (distance from the tibiotarsal articulation to the distal end of the toe IV), **FOL**=foot length (from the base of inner metatarsal tubercle to the tip of fourth toe), **TED**=tympanum-eye distance (from anterior edge of tympanum to posterior corner of the eye), **FDW**=finger disk width (width at the widest part of the disk of finger III), and **DPW**=distal phalanx width (maximal width of the distal phalanx of finger III).

To reduce the impact of allometry, a size-corrected value from the ratio of each character to SVL was calculated for the following morphometric analyses. Principal component analysis (PCAs) of size-corrected variables and simple bivariate scatterplots was used to explore and reflect the morphometric differences between the new species and *O. lipuensis*. Mann-Whitney *U* tests were used to test the significance of differences on morphometric characters between the new species and *O. lipuensis*, *O. kweichowensis* and *O. wuchuanensis*. Mann-Whitney *U* tests were also conducted to test the morphometric differences between the males and the females of the new species. The statistical analyses were performed using SPSS 21.0 (SPSS, Inc., Chicago. IL, USA), and differences were considered to be significant at $P < 0.05$.

Sex was determined by direct observation of calling behavior and the presence of internal vocal sac openings for males, as well as the presence of eggs on the abdomen for females. The presence or absence of nuptial pads/spines was examined by optical microscopy.

We compared the morphological characters of the new taxon with other species of *Odorrana*. Comparative data were obtained from the literature for 61 species of *Odorrana* (Table 3). For comparison, we examined the type and/or topotype materials for *O. lipuensis*, *O. kweichowensis*, and *O. wuchuanensis* (Appendix I).

3. Results

3.1. Phylogenetic analyses and genetic divergence The maximum likelihood (ML) and Bayesian inference (BI) phylogenetic trees were constructed based on concatenated DNA sequences of the mitochondrial 12S rRNA (752 bp), 16S rRNA (1006 bp), and ND2 (1030 bp) genes with a total length of 2788 bp. ML and BI analyses resulted in a largely identical topology (Figure 2). The new taxon is a sister taxon to *O. lipuensis* with high node support values (1.00 in BI and 100% in ML; Figure 2).

The smallest *p*-distance divergences between the new lineage and other species of *Odorrana* were 6.06% in 12S rRNA (between new taxon and *O. lipuensis*) and 3.90% in 16S rRNA (between new taxon and *O. geminata*), which were at the same divergence level as those among recognized congeners (1.94% and 2.79% in 12S rRNA between *O. wuchuanensis vs. O. mutschmanni* and *O. kweichowensis vs. O. schmackeri*, respectively; and 1.30% and 1.95% in 16S rRNA between *O. lungshengensis vs. O. yizhanggensis* and *O. nanjiangensis vs. O. hejiangensis*, respectively), indicating that the new taxon represents an independent evolutionary lineage (Tables S2–S3).

3.2. Morphological analyses The Mann-Whitney *U* tests indicated that males of the new species were significantly different from *O. lipuensis* and *O. kweichowensis* in many morphometric characters (all *P* values < 0.05; Table 4). PCA extracted three and four principal component factors with Eigenvalues greater than two in males and females, respectively (Table S4). The first two principal components explained 61.34% and 63.28%, of the total variation in males and females, respectively. These differences were mainly influenced by limb and head characteristics (Table S4). The new taxon was distinctly separated from *O. lipuensis* and *O. kweichowensis* on the two-dimensional plots of PC1 *vs.* PC2, in both males and females (Figure 3).

3.3. Taxonomic account

***Odorrana liboensis* sp. nov. (Tables 2 and 4, Figures 4–5)**

Holotype. GZNU20180608004 (Figure 4), adult male, collected by Tao LUO on June 8, 2018 from Maolan National Nature

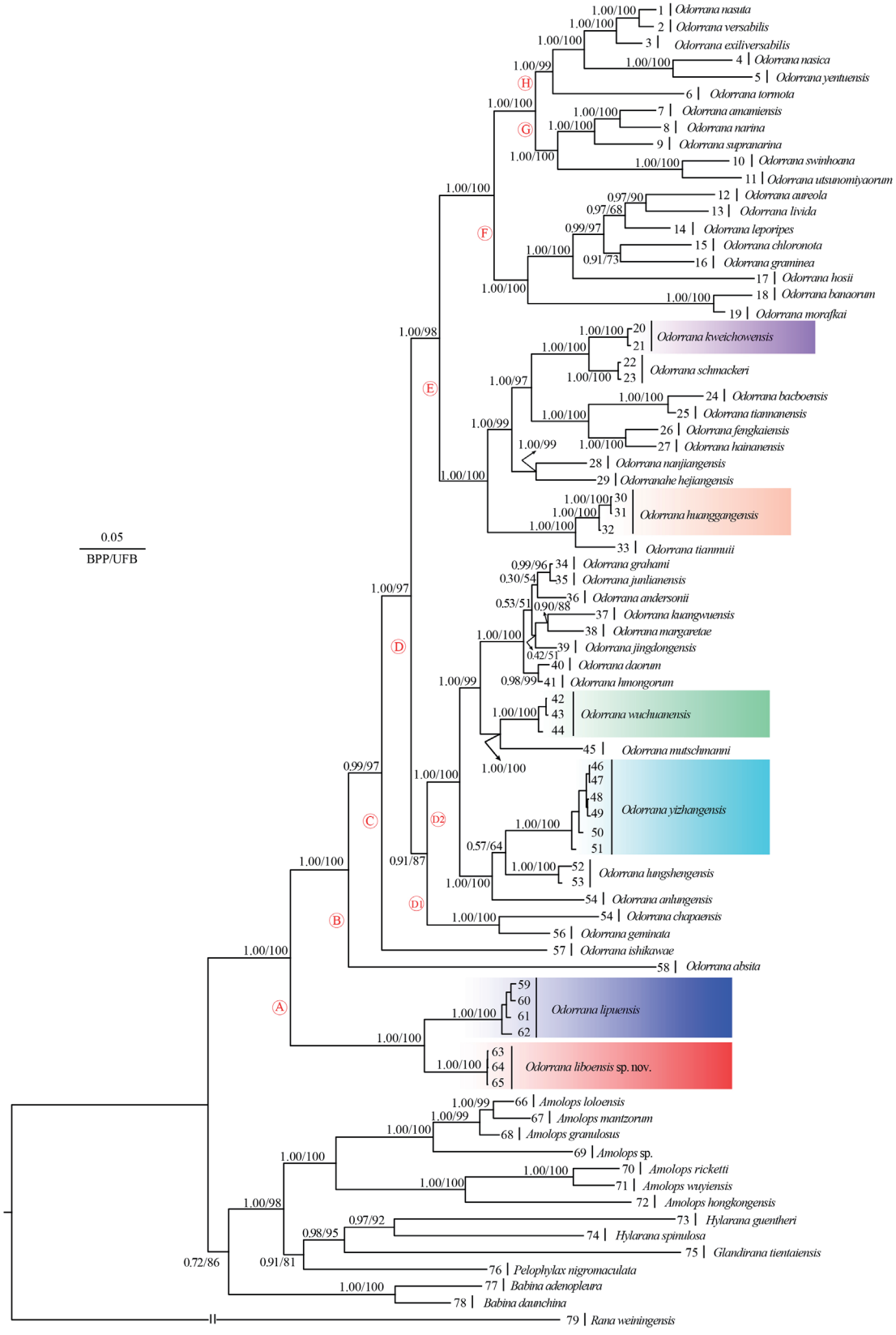

Figure 2 Phylogenetic tree based on mitochondrial 12S rRNA+16S rRNA+ND2 genes. In the phylogenetic tree, ultrafast bootstrap supports (UFB) from ML analyses and Bayesian posterior probabilities (BPP) from BI analyses were noted beside nodes. The scale bar represents 0.05 nucleotide substitutions per site. Numbers at the tips of branches correspond to the ID numbers in Table 1.

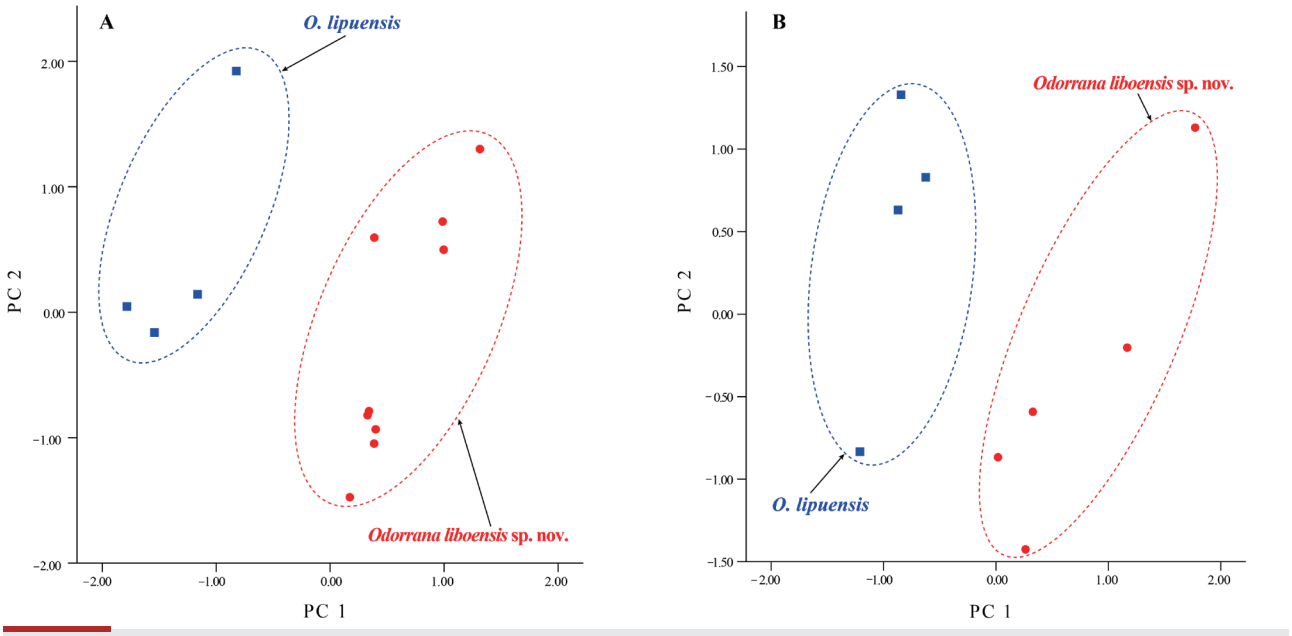

Figure 3 Plots of the first principal component (PC 1) versus the second (PC 2) for *Odorrana liboensis* **sp. nov**. and *O. lipuensis* from a principal component analysis. A, male. B, female.

Reserve (25.481711° N, 108.078003° E, ca. 715 m a.s.l.), Libo County, Guizhou Province, China.

Paratypes. Thirteen individuals collected at the same locality as the holotype. GZNU20180608002, GZNU20180608003, GZNU20180608006, GZNU20180608007, GZNU20180608009, GZNU20180608010, GZNU20180608011 and GZNU20180608012, adult males collected by Tao Luo on June 8; GZNU20180815001 (Figure 5), adult females collected by Xiang ZENG on August 15, 2018; GZNU20160802001, GZNU20160802002, GZNU20160802003, and GZNU20160729009, adult females collected by Tao Luo on August 2, 2016.

Etymology. The specific epithet "*liboensis*" is in reference to the type locality of the new species: Libo County, Guizhou Province, China. We propose the common English name "Libo Odorous Frog" and Chinese name "Li Bo Chou Wa (荔波臭蛙)".

Differential diagnosis. *Odorrana liboensis* **sp. nov.** is assigned to genus *Odorrana* based upon molecular phylogenetic analyses and the following morphological characters: (1) dorsum is mostly green; (2) tips of digits dilated, tapering, disks with circum-marginal grooves or lateroventral grooves, and vertical diameter longer than horizontal diameter in the disks; (3) supernumerary tubercle below the base of fingers III and IV; (4) feet fully webbed to disks, without tarsal fold; (5) the first finger thick and nuptial pad distinct and (6) dorsal skin smooth, dorsolateral folds absent or fine (Fei *et al*., 2009; Li *et al*., 2018a).

Odorrana liboensis **sp. nov.** is distinguished from congeners by a combination of the following characters: (1) having medium body size, with the snout-vent length (SVL) of adult females approximately 1.2 times as long as that of males at 56.9 ± 1.0 (55.8–58.2 mm, n = 9) in females and 48.7 ± 1.2 (47.1–49.9 mm, n = 5) in males; (2) head length greater than width in males and females; (3) tympanum distinctly visible, greater than one-half the diameter of the eye; (4) eyes big and prominent, with the width of the upper eyelid (UEW) approximately 3/4 of the eye diameter (ED); (5) dorsolateral folds absent; (6) two metacarpal tubercles; (7) relative finger lengths: II < I < IV < III; (8) subarticular tubercles on fingers prominent: 1, 1, 2, 2; (9) one metatarsal tubercle; (10) tibiotarsal articulation reaching to between the eye and the nostril when the leg is stretched forward; (11) toes with entire webbing to disks; (12) subarticular tubercles on toes prominent: 1, 1, 2, 3, 2; (13) dorsal surfaces of limbs with distinct brownish-black bands; (14) smooth, grass-green dorsum with irregular brown mottling; (15) venter smooth, lacking black spots; and (16) lacking pectoral spinules, lacking vocal sacs, and a light white nuptial pad present on finger I in males.

Description of holotype. GZNU 20180608004 (Figure 4), adult male. Medium body size, SVL 49.8 mm; habitus slender; head length slightly larger than head width (HDL=17.6 mm; HDW=15.6 mm; HDL/HDW 1.12); snout short, rounded, and projecting beyond the lower jaw in dorsal view, longer than the diameter of the eye (SL/ED 1.30); nostril rounded, distinct, closer to the snout tip than the eye (NEL/NSL 0.52); internasal distance less than interorbital distance (IND/IOD 0.91) and greater than upper eyelid width (IND/UEW 1.06); pineal body invisible; tympanum distinct, rounded, 75% of eye diameter, depressed relative to the skin of the temporal region, tympanic rim slightly elevated relative to tympanum; vomerine teeth

Table 3 References for morphological characters for congeners of the genus *Odorrana*.

ID	Species	Literature obtained
1	*Odorrana absita* (Stuart & Chan-ard, 2005)	Stuart and Chan-ard (2005)
2	*Odorrana amamiensis* (Matsui, 1994)	Matsui (1994)
3	*Odorrana andersonii* (Boulenger, 1882)	Boulenger (1882)
4	*Odorrana anlungensis* (Liu & Hu, 1973)	Hu *et al.* (1973)
5	*Odorrana aureola* Stuart, Chuaynkern, Chan-ard & Inger, 2006	Stuart *et al.* (2006)
6	*Odorrana bacboensis* (Bain, Lathrop, Murphy, Orlov & Ho, 2003)	Bain *et al.* (2003)
7	*Odorrana banaorum* (Bain, Lathrop, Murphy, Orlov & Ho, 2003)	Bain *et al.* (2003)
8	*Odorrana bolavensis* (Stuart & Bain, 2005)	Stuart and Bain (2005)
9	*Odorrana cangyuanensis* (Yang, 2008)	Yang (2008)
10	*Odorrana chapaensis* (Bourret, 1937)	Bourret (1937)
11	*Odorrana chloronota* (Günther, 1876)	Günther (1876)
12	*Odorrana dulongensis* Liu, Che & Yuan, 2021	Liu *et al.* (2021)
13	*Odorrana exiliversabilis* Li, Ye & Fei, 2001	Fei *et al.* (2001b)
14	*Odorrana fengkaiensis* Wang, Lau, Yang, Chen, Liu, Pang & Liu, 2015	Wang *et al.* (2015)
15	*Odorrana geminata* Bain, Stuart, Nguyen, Che & Rao, 2009	Bain *et al.* (2009)
16	*Odorrana gigatympana* (Orlov, Ananjeva & Ho, 2006)	Orlov *et al.* (2006)
17	*Odorrana grahami* (Boulenger, 1917)	Boulenger (1917)
18	*Odorrana graminea* (Boulenger, 1900)	Boulenger (1900)
19	*Odorrana hainanensis* Fei, Ye & Li, 2001	Fei *et al.* (2001a)
20	*Odorrana hejiangensis* (Deng & Yu, 1992)	Deng *et al.* (1992)
21	*Odorrana hosii* (Boulenger, 1891)	Boulenger (1891)
22	*Odorrana huanggangensis* Chen, Zhou & Zheng, 2010	Chen *et al.* (2010a)
23	*Odorrana ichangensis* Chen, 2020	Shen et al. (2020)
24	*Odorrana indeprensa* (Bain & Stuart, 2006)	Bain and Stuart (2005)
25	*Odorrana ishikawae* (Stejneger, 1901)	Stejneger (1901)
26	*Odorrana jingdongensis* Fei, Ye & Li, 2001	Fei *et al.* (2001a)
27	*Odorrana junlianensis* Huang, Fei & Ye, 2001	Ye and Fei (2001)
28	*Odorrana khalam* (Stuart, Orlov & Chan-ard, 2005)	Stuart and Chan-ard (2005)
29	*Odorrana kuangwuensis* (Liu & Hu, 1966)	Hu *et al.* (1966)
30	*Odorrana kweichowensis* Li, Xu, Lv, Jiang, Wei & Wang, 2018	Li *et al.* (2018a)
31	*Odorrana leporipes* (Werner, 1930)	Werner (1930)
32	*Odorrana lipuensis* Mo, Chen, Wu, Zhang & Zhou, 2015	Mo *et al.* (2015)
33	*Odorrana livida* (Blyth, 1856)	Blyth (1856)
34	*Odorrana lungshengensis* (Liu & Hu, 1962)	Liu and Hu (1962)
35	*Odorrana macrotympana* (Yang, 2008)	Yang (2008)
36	*Odorrana margaretae* (Liu, 1950)	Liu (1950)
37	*Odorrana mawphlangensis* (Pillai & Chanda, 1977)	Pillai Chanda (1977)
38	*Odorrana monjerai* (Matsui & Jaafar, 2006)	Matsui and Jaafar (2006)
39	*Odorrana morafkai* (Bain, Lathrop, Murphy, Orlov & Ho, 2003)	Bain *et al.* (2003)
40	*Odorrana mutschmanni* Pham, Nguyen, Le, Bonkowski & Ziegler, 2016	Pham *et al.* (2016)
41	*Odorrana nanjiangensis* Fei, Ye, Xie & Jiang, 2007	Fei *et al.* (2007a)
42	*Odorrana narina* (Stejneger, 1901)	Stejneger (1901)
43	*Odorrana nasica* (Boulenger, 1903)	Boulenger (1903)
44	*Odorrana nasuta* Li, Ye & Fei, 2001	Fei *et al.* (2001b)
45	*Odorrana orba* (Stuart & Bain, 2005)	Stuart and Bain (2005)
46	*Odorrana rotodora* (Yang & Rao, 2008)	Yang (2008)
47	*Odorrana schmackeri* (Boettger, 1892)	Boettger (1892)
48	*Odorrana sinica* (Ahl, 1927)	Ahl (1927)
49	*Odorrana splendida* Kuramoto, Satou, Oumi, Kurabayashi & Sumida, 2011	Kuramoto *et al.* (2011)
50	*Odorrana supranarina* (Matsui, 1994)	Matsui (1994)
51	*Odorrana swinhoana* (Boulenger, 1903)	Boulenger (1903)
52	*Odorrana tianmuii* Chen, Zhou & Zheng, 2010	Chen *et al.* (2010b)
53	*Odorrana tiannanensis* (Yang & Li, 1980)	Yang and Li (1980)
54	*Odorrana tormota* (Wu, 1977)	Wu (1977)
55	*Odorrana trankieni* (Orlov, Le & Ho, 2003)	Orlov *et al.* (2003)
56	*Odorrana utsunomiyaorum* (Matsui, 1994)	Matsui (1994)
57	*Odorrana versabilis* (Liu & Hu, 1962)	Li and Hu (1962)
58	*Odorrana wuchuanensis* (Xu, 1983)	Wu *et al.* (1983)
59	*Odorrana yentuensis* Tran, Orlov & Nguyen, 2008	Tran *et al.* (2008)
60	*Odorrana yizhangensis* Fei, Ye & Jiang, 2007	Fei *et al.* (2007b)
61	*Odorrana zhaoi* Li, Lu & Rao, 2008	Li *et al.* (2008)

moderately developed, on two oblique ridges; tongue cordiform, deeply notched posteriorly; and eyes large, slightly protuberant in dorsal view, eye diameter 26.70% of head length, pupils transverse; supratympanic fold absent.

Forelimbs are slender and comparatively short, the length of the lower arm and hand is 41.97% of SVL; fingers slender, relative finger lengths: I<II<IV<III; tips of all except first finger expanded with circummarginal grooves, horizontal grooves present, without lateral fringes; width of finger III disc about 68.57% the diameter of tympanum; webbing absent; subarticular tubercles prominent: 1, 1, 2, 2; inner metacarpal tubercle oval, elongate; outer metacarpal tubercle oval; and light white nuptial pads present.

Hindlimbs are slender (HLL/SVL 1.86); heels overlapping

when thighs are positioned at right angles to the body; tibiotarsal articulation reaching the between eye to nostril when leg stretched forward; foot length less than tibia length (FL/TL 0.87); relative toe lengths I<II<III<V<IV; tips of toes expanded into disc with circummarginal grooves; subarticular tubercles prominent: 1, 1, 2, 3, 2; toes with entire webbing to disks; elongate, oval inner metatarsal tubercle, larger than toe I; and outer metatarsal tubercle absent.

Skin is smooth on upper surfaces; venter smooth; tiny spinules on lateral body, upper edge of lid, temporal region, and

Figure 4 Morphological features of the live adult male holotype GZNU20180608004 of *Odorrana liboensis* **sp. nov.** and *O. wuchuanensis*. (A) Dorsal view; (B) Ventral view; (C) Dorsolateral view; (D) Tadpole; (E) Type locality of *Odorrana liboensis* **sp. nov.** in June, 2018 (dry season); (F) Dorsolateral view of *O. wuchuanensis* in life.

anterior and posterior edge of tympanum; weak supratympanic fold from the posterior edge of the eye to the posterior edge of the tympanum; and dorsolateral fold absent.

Coloration of holotype in life (Figure 4). Dorsal parts of head and dorsum, flank, forelimb, thigh, tibia, and foot are grass-green with irregular brown mottling; the throat, chest, and abdomen lack black spots; dorsal surfaces of limbs have indistinct brownish-black bands, the thighs with four brownish-black bands and tibias with three; ventral surface of the limbs is pink; the iris is black, surrounded by a gold-green network; and the tympanum is dark brown.

Preserved holotype coloration. After preservation in 75% ethanol, the dorsal surface of the body coloration changed to dark brown grey; the dorsal surface of the head coloration changed to dark grey; the transverse bands on limbs and digits were not distinct and the coloration changed to lighter colors; the throat was light grayish yellow; the chest was light ash black; the belly was light gray-white; the posterior of ventral surface of body, inner thigh, and upper part of the tibia were creamy yellow; the palms and metatarsal tubercles were ash black; and the ventral surface of the forelimbs and hindlimbs were creamy yellow with brown mottling.

Table 4 Morphological comparison of *Odorrana liboensis* **sp. nov.** (OB), *O. lipuensis* (OP), *O. kweichowensis* (OK), and *O. wuchuanensis* (OW). All units are in mm. *P*-values are at 95% significance. Morphometric characters are explained in the methods section. BM and BF are the abbreviations for male and female from *Odorrana liboensis* **sp. nov.**

Measure-ments	*Odorrana liboensis* **sp. nov.**				*Odorrana lipuensis*				*Odorrana wuchuanensis*			
	Male (*n* = 5)		Female (*n* =9)		Male (*n* =4)		Female (*n* =4)		Male (*n* =12)		Female (*n* =5)	
	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD
SVL	47.1–49.9	48.7 ± 1.2	55.8–58.2	56.9 ± 1.0	40.7–47.7	43.1 ± 3.1	49.9–54.1	52.2 ± 1.8	70.0–80.5	101.9 ± 2.5	99.8–105.7	76.8 ± 3.2
HDL	16.7–18.4	17.5 ± 0.6	19.3–21.5	20.7 ± 0.8	14.6–15.6	15.0 ± 0.4	17.2–19.7	18.6 ± 1.2	22.6–28.9	32.4 ± 1.6	29.9–34.1	26.2 ± 1.7
HDW	13.8–15.6	14.9 ± 0.6	18.2–19.5	18.9 ± 0.5	13.2–14.6	13.7 ± 0.6	17.3–20.5	18.3 ± 1.5	21.7–28.2	33.8 ± 3.8	30.9–40.0	24.4 ± 1.6
SL	6.5–8.2	7.3 ± 0.5	8.5–9.5	9.0 ± 0.4	5.6–6.6	6.1 ± 0.5	7.9–8.2	8.1 ± 0.2	9.4–17.8	13.2 ± 1.9	10.3–15.5	12.6 ± 2.2
IND	4.8–5.6	5.2 ± 0.3	5.3–6.8	6.1 ± 0.7	3.6–4.5	4.2 ± 0.4	4.5–5.5	5.0 ± 0.5	7.4–10.0	10.5 ± 0.5	9.8–11.1	8.7 ± 0.7
NED	3.1–4.5	3.7 ± 0.5	5.2–6.6	5.9 ± 0.5	3.5–4.3	3.7 ± 0.4	4.6–5.2	4.8 ± 0.3	7.6–8.5	9.1 ± 0.5	8.3–9.6	8.0 ± 0.3
NSD	2.8–4	3.4 ± 0.4	2.7–3.3	3.1 ± 0.3	2.2–3.2	2.8 ± 0.5	2.9–3.7	3.3 ± 0.4	3.9–7.3	5.3 ± 0.6	4.3–5.9	4.7 ± 1.0
IOD	4.6–6.8	6.0 ± 0.8	7.2–7.9	7.5 ± 0.3	3.2–4.1	3.7 ± 0.4	4.7–5.6	5.0 ± 0.4	5.8–13.5	6.6 ± 1.2	5.1–8.3	8.0 ± 2.1
IFE	8.3–9.6	9.3 ± 0.4	10.2–12.2	11.2 ± 0.8	6.8–8.3	7.5 ± 0.7	8.5–9.5	9.0 ± 0.4	12.4–15.9	11.6 ± 1.1	10.5–13.3	13.6 ± 1.1
IAE	14.3–15.3	14.7 ± 0.3	15.2–17.3	16.0 ± 0.9	9.9–11.4	10.5 ± 0.6	12.9–14.9	14.0 ± 0.9	22.5–29.9	29.4 ± 0.8	28.5–30.5	26.9 ± 2.7
UEW	3.5–4.8	4.1 ± 0.4	4.4–5.1	4.8 ± 0.3	3.2–4.0	3.6 ± 0.3	4.7–5.2	5.0 ± 0.2	4.5–10.5	7.3 ± 1.8	4.3–9.0	6.4 ± 1.5
ED	4.7–6.5	5.6 ± 0.6	5.5–6.9	6.4 ± 0.5	4.3–5.5	4.7 ± 0.6	5.1–6.5	5.9 ± 0.6	6.7–13.3	9.6 ± 1.5	6.9–10.7	8.6 ± 1.7
TD	3.1–3.8	3.5 ± 0.3	4.8–5.9	5.1 ± 0.4	3.2–4.1	3.6 ± 0.4	3.8–5.1	4.4 ± 0.6	4.6–10.9	6.5 ± 1.9	3.5–8.4	6.4 ± 1.6
LAHL	20.5–22.6	21.2 ± 0.6	28.2–29.7	29.0 ± 0.7	17.8–22.4	19.7 ± 2.1	25.6–27.8	26.5 ± 0.9	32.3–41.7	49.1 ± 2.4	46.4–51.8	38.6 ± 2.5
LAN	3–4.7	3.7 ± 0.6	3.5–5.1	4.2 ± 0.6	3.7–5.0	4.3 ± 0.6	3.2–4.8	3.7 ± 0.8	4.6–10.9	9.1 ± 0.5	8.4–9.7	8.3 ± 1.6
HAL	11.2–12.8	12.4 ± 0.5	12.1–14.4	13.2 ± 1.0	10.3–12.8	11.6 ± 1.0	14.1–15.8	14.7 ± 0.8	24.8–29.5	29.4 ± 0.5	28.9–29.9	27.9 ± 1.5
HLL	86.8–102.7	92.7 ± 5.9	102.7–111.5	106.8 ± 4.0	68.2–76.9	73.1 ± 3.7	26.2–27.9	27.4 ± 0.8	103.5–140.2	164.7 ± 7.5	158.9–177.7	129.0 ± 8.8
TL	26.4–35.8	30.7 ± 3.2	31.1–41.5	36.3 ± 4.5	21.6–24.5	23.3 ± 1.3	26.5–28.9	27.7 ± 1.0	33.5–48.2	51.7 ± 0.7	50.7–52.5	44.6 ± 3.7
TW	6.3–6.9	6.6 ± 0.2	6.3–7.6	7.0 ± 0.5	3.9–5.6	4.8 ± 0.7	4.6–6.6	5.3 ± 0.9	7.8–42.4	9.3 ± 0.3	8.9–9.8	22.0 ± 16.8
TFL	35.4–38.7	37.3 ± 1.2	42.2–48.5	44.2 ± 2.6	30.9–33.8	31.8 ± 1.3	26.1–38.6	35.0 ± 6.0	40.3–48.7	44.4 ± 2.0	40.9–45.9	44.7 ± 2.5
FOL	24.5–26.9	26.2 ± 0.7	27.2–31.3	28.9 ± 1.7	19.5–23.0	21.3 ± 1.5	25.4–26.8	26.3 ± 0.6	32.4–46.3	51.5 ± 2.0	48.5–53.4	42.1 ± 3.9
TED	1.9–2.2	2.1 ± 0.1	2.1–3.4	2.7 ± 0.5	1.3–1.5	1.4 ± 0.1	1.8–2.3	2.1 ± 0.2	2.9–4.6	4.5 ± 0.8	3.4–5.1	3.7 ± 0.5
FDW	2.1–2.5	2.3 ± 0.2	2.5–3.1	2.8 ± 0.3	1.2–2.0	1.6 ± 0.3	1.7–2.6	2.1 ± 0.4	3.1–6.7	4.9 ± 0.5	4.2–5.5	4.4 ± 1.1
DPW	2.5–2.8	2.6 ± 0.1	2.2–2.8	2.4 ± 0.3	1.1–1.6	1.4 ± 0.2	1.7–2.3	2.0 ± 0.3	1.4–7.7	5.9 ± 0.5	5.2–6.5	5.1 ± 1.6
HDL/SVL	0.34–0.39	0.36 ± 0.02	0.33–0.37	0.36 ± 0.02	0.33–0.36	0.35 ± 0.02	0.33–0.37	0.36 ± 0.02	0.32–0.38	0.32 ± 0.01	0.30–0.33	0.34 ± 0.02
HDW/SVL	0.28–0.33	0.31 ± 0.02	0.32–0.34	0.33 ± 0.01	0.31–0.33	0.32 ± 0.01	0.33–0.38	0.35 ± 0.02	0.30–0.37	0.33 ± 0.03	0.31–0.39	0.32 ± 0.02
HDL/HDW	1.13–1.23	1.17 ± 0.04	1.01–1.15	1.10 ± 0.05	1.07–1.14	1.10 ± 0.03	0.96–1.07	1.02 ± 0.05	0.99–1.15	0.97 ± 0.08	0.85–1.06	1.08 ± 0.05
SL/SVL	0.13–0.17	0.15 ± 0.01	0.15–0.16	0.16 ± 0.00	0.13–0.16	0.14 ± 0.01	0.15–0.16	0.16 ± 0.00	0.13–0.24	0.13 ± 0.02	0.10–0.15	0.16 ± 0.03
SL/HDL	0.38–0.45	0.42 ± 0.03	0.41–0.49	0.43 ± 0.03	0.38–0.45	0.41 ± 0.03	0.42–0.48	0.44 ± 0.03	0.42–0.61	0.40 ± 0.04	0.34–0.45	0.48 ± 0.06
IOD/HDW	0.31–0.47	0.40 ± 0.06	0.39–0.41	0.40 ± 0.01	0.24–0.31	0.27 ± 0.03	0.23–0.31	0.27 ± 0.03	0.25–0.48	0.19 ± 0.03	0.16–0.22	0.32 ± 0.07
IND/IOD	0.73–1.21	0.89 ± 0.15	0.74–0.92	0.81 ± 0.07	0.88–1.31	1.13 ± 0.18	0.84–1.15	1.00 ± 0.15	0.57–1.42	1.63 ± 0.29	1.33–2.10	1.14 ± 0.23
ED/TD	1.34–2.02	1.63 ± 0.21	1.10–1.35	1.26 ± 0.13	1.23–1.50	1.33 ± 0.12	1.16–1.44	1.35 ± 0.13	1.21–1.52	1.53 ± 0.29	1.22–1.98	1.35 ± 0.11
ED/HDL	0.27–0.36	0.32 ± 0.03	0.29–0.32	0.31 ± 0.01	0.28–0.35	0.31 ± 0.03	0.30–0.34	0.32 ± 0.02	0.26–0.46	0.29 ± 0.04	0.23–0.33	0.33 ± 0.05
TD/HDL	0.17–0.22	0.20 ± 0.01	0.23–0.28	0.25 ± 0.02	0.22–0.26	0.24 ± 0.02	0.22–0.26	0.24 ± 0.02	0.17–0.38	0.20 ± 0.05	0.12–0.25	0.24 ± 0.05
HAL/SVL	0.22–0.27	0.25 ± 0.01	0.22–0.26	0.23 ± 0.02	0.25–0.29	0.27 ± 0.02	0.27–0.29	0.28 ± 0.01	0.33–0.41	0.29 ± 0.00	0.28–0.29	0.36 ± 0.03
HLL/SVL	1.75–2.17	1.91 ± 0.14	1.83–1.92	1.88 ± 0.05	1.56–1.85	1.70 ± 0.12	0.51–0.53	0.52 ± 0.01	1.28–1.85	1.62 ± 0.09	1.54–1.78	1.68 ± 0.14
TED/HDL	0.11–0.13	0.12 ± 0.01	0.10–0.16	0.13 ± 0.02	0.08–0.10	0.09 ± 0.01	0.10–0.12	0.11 ± 0.01	0.11–0.17	0.14 ± 0.03	0.10–0.16	0.14 ± 0.02

(Continued Table 4)

Measurements	*Odorrana kweichowensis*				*P*-value from Mann-Whitney *U* test						
	Male (*n* = 18)		Female (*n* = 17)		Male			Female			
	Range	Mean ± SD	Range	Mean ± SD	OB *vs.* OP	OB *vs.* OW	OB *vs.* OK	OB *vs.* OP	OB *vs.* OW	OB *vs.* OK	BM *vs.* BF
SVL	42.4–48.8	44.8 ± 1.8	79.4–94.0	85.5 ± 4.7	0.007	0.000	0.000	0.016	0.008	0.000	0.001
HDL	15.1–17.9	16.3 ± 0.8	25.7–31.4	28.0 ± 1.6	0.001	0.034	0.463	0.111	0.008	0.002	1.000
HDW	11.3–13.4	12.0 ± 0.5	20.7–25.1	22.3 ± 1.2	0.007	0.382	0.000	0.063	0.421	0.000	0.004
SL	6.0–7.7	7.0 ± 0.5	11.7–16.0	12.8 ± 1.1	0.004	0.193	0.131	0.730	0.008	0.101	0.112
IND	4.2–5.7	5.0 ± 0.5	8.1–11.8	9.3 ± 1.1	0.001	0.129	0.322	0.190	0.548	0.820	1.000
NED	3.2–4.3	3.8 ± 0.3	6.1–9.3	7.2 ± 0.9	1.000	0.000	0.053	0.111	0.032	0.001	0.001
NSD	3.1–3.9	3.3 ± 0.2	5.3–7.8	5.9 ± 0.6	0.019	0.041	0.059	0.016	0.690	0.000	0.001
IOD	3.9–5.4	4.4 ± 0.4	3.9–10.7	8.1 ± 1.5	0.001	0.015	0.000	0.016	0.008	0.000	0.364
IFE	4.0–7.7	5.9 ± 1.0	9.9–15.3	12.6 ± 1.5	0.001	0.082	0.000	0.016	0.008	0.000	0.052
IAE	5.6–10.0	7.9 ± 1.6	16.5–20.8	18.2 ± 1.3	0.001	0.001	0.000	0.413	0.421	0.000	0.042
UEW	3.5–4.6	3.9 ± 0.3	4.5–5.9	5.3 ± 0.4	0.190	0.422	0.527	0.016	0.056	0.000	0.797
ED	4.9–6.5	5.5 ± 0.5	8.1–10.2	9.0 ± 0.5	0.042	0.310	0.145	1.000	0.095	0.048	0.797
TD	3.1–4.4	3.6 ± 0.3	3.8–5.4	4.6 ± 0.4	0.699	0.018	0.020	0.286	0.008	0.000	0.001
LAHL	20.4–25.0	22.4 ± 1.2	38.6–45.0	41.5 ± 1.8	0.298	0.001	0.000	0.905	0.095	0.120	0.001
LAN	3.3–5.6	4.5 ± 0.6	6.2–9.6	7.2 ± 0.9	0.019	0.001	0.001	0.556	0.032	0.048	0.898
HAL	11.2–14.5	13.1 ± 0.9	21.1–26.0	23.8 ± 1.3	0.240	0.000	0.000	0.016	0.008	0.000	0.029
HLL	75.2–87.5	81.6 ± 3.6	139.3–161.1	152.3 ± 6.6	0.001	0.000	0.194	0.016	0.008	0.015	0.797
TL	21.7–29.1	24.7 ± 1.8	47.2–54.0	50.0 ± 1.9	0.001	0.129	0.002	0.032	0.008	0.319	1.000
TW	4.4–6.5	5.1 ± 0.5	9.3–13.2	10.5 ± 1.2	0.001	0.554	0.000	0.111	0.008	1.000	0.019
TFL	32.1–38.9	35.7 ± 1.9	63.5–73.0	68.3 ± 2.8	0.001	0.000	0.085	0.016	0.008	0.085	1.000
FOL	21.6–26.3	23.8 ± 1.4	38.0–47.7	43.2 ± 2.6	0.001	0.082	0.232	0.730	0.841	0.880	0.083
TED	1.7–2.5	2.0 ± 0.2	2.8–3.9	3.4 ± 0.3	0.001	0.095	0.212	0.286	0.690	0.085	0.797
FDW	1.3–2.1	1.7 ± 0.2	2.4–3.6	2.9 ± 0.3	0.001	0.111	0.000	0.190	0.841	0.000	0.699
DPW	1.3–1.9	1.6 ± 0.2	2.2–3.3	2.7 ± 0.3	0.001	0.001	0.000	0.190	0.008	0.000	0.001
HDL/SVL	0.33–0.38	0.36 ± 0.01	0.31–0.35	0.33 ± 0.01	0.898	0.034	0.463	0.111	0.008	0.002	1.000
HDW/SVL	0.25–0.29	0.27 ± 0.01	0.24–0.27	0.26 ± 0.01	0.083	0.382	0.000	0.063	0.421	0.000	0.004
HDL/HDW	1.22–1.47	1.36 ± 0.06	1.17–1.30	1.25 ± 0.03	0.007	0.000	0.000	0.063	0.032	0.000	0.007
SL/SVL	0.12–0.18	0.16 ± 0.01	0.14–0.17	0.15 ± 0.01	0.699	0.193	0.131	0.730	0.008	0.101	0.112
SL/HDL	0.34–0.49	0.43 ± 0.04	0.44–0.51	0.46 ± 0.02	0.898	0.002	0.253	1.000	0.421	0.039	0.518
IOD/HDW	0.33–0.40	0.37 ± 0.02	0.19–0.47	0.36 ± 0.06	0.001	0.015	0.085	0.016	0.008	0.410	0.364
IND/IOD	0.91–1.43	1.14 ± 0.15	0.91–2.17	1.19 ± 0.28	0.029	0.006	0.000	0.063	0.008	0.000	0.438
ED/TD	1.31–1.82	1.55 ± 0.18	1.58–2.54	1.96 ± 0.20	0.012	0.001	0.322	0.413	0.056	0.000	0.007
ED/HDL	0.29–0.39	0.34 ± 0.03	0.28–0.35	0.32 ± 0.02	1.000	0.972	0.118	0.730	0.548	0.140	0.438
TD/HDL	0.18–0.25	0.22 ± 0.02	0.13–0.19	0.17 ± 0.01	0.002	0.001	0.005	0.283	0.056	0.000	0.001
HAL/SVL	0.26–0.34	0.29 ± 0.02	0.26–0.33	0.28 ± 0.02	0.060	0.000	0.000	0.016	0.008	0.000	0.029
HLL/SVL	1.63–2.02	1.82 ± 0.10	1.67–1.97	1.78 ± 0.08	0.001	0.000	0.194	0.016	0.008	0.015	0.797
TED/HDL	0.10–0.14	0.13 ± 0.01	0.10–0.14	0.12 ± 0.01	0.001	0.003	0.176	0.286	0.690	0.543	0.438

Variations. The basic statistics for measurements are presented in Table 2. In life, all paratypes matched the overall basic morphological characters of the holotype. Females (SVL 56.9 ± 1.0 mm, *n* = 5) have larger body size than males (SVL 48.7 ± 1.2 mm, *n* = 9), with the SVL in females approximately 1.2 times that in males, but the relative sizes of ED and TD are obviously larger in males than in females (Table 4); the dorsal surfaces of limbs with indistinct brownish-black bands (Figure 5).

Sexual dimorphism. Adult females have an SVL of 55.8–58.2 mm, larger than adult males, with an SVL of 47.1–49.9 mm. Adult males lack vocal sacs. In breeding, light white nuptial pads are present on finger I in males.

Comparisons. Comparative data of *Odorrana liboensis* **sp. nov.** with 61 recognized congeners of *Odorrana* are given in Table S5. By having medium body size (minimum SVL > 47.0 mm in males), *Odorrana liboensis* **sp. nov.** differs from *O. absita*, *O. anlungensis*, *O. gigatympana*, *O. huanggangensis*, *O. khalam*, *O. kweichowensis*, *O. monjerai*, *O. morafkai*, *O. nasica*, *O. orba*, and *O. tormota* (*vs.* maximum SVL < 47.0 mm in males). By having medium body size (maximum SVL < 50.0 mm in males), *Odorrana liboensis* **sp. nov.** differs from *O. amamiensis*, *O. andersonii*, *O. aureola*, *O. bacboensis*, *O. cangyuanensis*, *O. chapaensis*, *O. geminata*, *O. grahami*, *O. hainanensis*, *O. hosii*, *O. ishikawae*, *O. jingdongensis*, *O. junlianensis*, *O. kuangwuensis*, *O. leporipes*,

O. livida, *O. lungshengensis*, *O. macrotympana*, *O. margaretae*, *O. mutschmanni*, *O. nanjiangensis*, *O. nasuta*, *O. sinica*, *O. splendida*, *O. supranarina*, *O. swinhoana*, *O. tiannanensis*, *O. trankieni*, *O. versabilis*, *O. wuchuanensis*, and *O. zhaoi* (*vs.* minimum SVL > 50.0 mm).

By having medium body size (*vs.* maximum SVL < 59.0 mm in females), *Odorrana liboensis* **sp. nov.** differs from *O. amamiensis*, *O. andersonii*, *O. anlungensis*, *O. aureola*, *O. bacboensis*, *O. banaorum*, *O. bolavensis*, *O. chapaensis*, *O. chloronota*, *O.dulongensis*, *O. fengkaiensis*, *O. geminata*, *O. grahami*, *O. hainanensis*, *O. hejiangensis*, *O. hosii*, *O. huanggangensis*, *O. ishikawae*, *O. jingdongensis*, *O. junlianensis*, *O. kuangwuensis*, *O. kweichowensis*, *O. livida*, *O. lungshengensis*, *O. macrotympana*, *O. margaretae*, *O. monjerai*, *O. morafkai*, *O. mutschmanni*, *O. nanjiangensis*, *O. narina*, *O. nasuta*, *O. orba*, *O. rotodora*, *O. schmackeri*, *O. splendida*, *O. supranarina*, *O. swinhoana*, *O. tianmuii*, *O. tiannanensis*, *O. tormota*, *O. versabilis*, *O. wuchuanensis*, *O. yentuensi*, *O. yizhangensis*, and *O. ichangensis* (*vs.* maximum SVL > 59.0 mm).

By lacking dorsolateral folds, *Odorrana liboensis* **sp. nov.** differs from *O. absita*, *O. amamiensis*, *O. banaorum*, *O. bolavensis*, *O. exiliversabilis*, *O. gigatympana*, *O. graminea*, *O. hosii*, *O. indeprensa*,

Figure 5 Morphological features of the live adult female GZNU20180815001 of *Odorrana liboensis* **sp. nov.** (A) Dorsal view; (B) Dorsolateral view; (C) Ventral view; (D) Ventral view of right foot; (E) Ventral view of right hand; (F) The entrance habitat of the karst cave at the type locality of *Odorrana liboensis* **sp. nov.**; (G) Water outlet in the cave.

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. yentuensis*, and *O. zhaoi* (*vs.* present).

By the tibiotarsal articulation reaching to between the eye and the nostril when the leg is stretched forward, *Odorrana liboensis* **sp. nov.** differs from *O. bacboensis*, *O. jingdongensis*, *O. lungshengensis*, *O. margaretae*, *O. mutschmanni*, *O. nanjiangensis*, *O. narina*, *O. orba*, *O. sinica*, *O. swinhoana*, *O. tormota*, and *O. yizhangensis* (*vs.* reaching the tip of the snout), from *O. nasica* and *O. nasuta* (*vs.* reaching the tip of the snout or a little beyond), from *O. hainanensis* (*vs.* reaching the tip of the snout or the anterior corner of eye), from *O. junlianensis* (*vs.* reaching the tip of the snout or between the nostril and the snout), from *O. cangyuanensis*, *O. exiliversabilis*, *O. fengkaiensis*, *O. gigatympana*, *O. grahami*, *O. graminea*, *O. tiannanensis*, *O. versabilis*, *O. yentuensis*, and *O. zhaoi* (*vs.* reaching to or beyond the tip of the snout), from *O. amamiensis* (*vs.* reaching far beyond the tip of the snout), from *O. amamiensis*, *O. anlungensis*, *O. huanggangensis*, *O. kuangwuensis*, *O. macrotympana*, *O. wuchuanensis*, and *O. ichangensis* (*vs.* reaching the nostril or beyond the tip of the snout), from *O. lipuensis*, *O. splendida*, and *O. supranarina* (*vs.* reaching the anterior corner of the eye), from *O. rotodora* and *O. trankieni* (*vs.* reaching beyond the eye), and from *O. utsunomiyaorum* (*vs.* reaching between the anterior corner of the eye and the nostril).

By lacking black bars on the lips, *Odorrana liboensis* **sp. nov.** differs from *O. andersonii*, *O. anlungensis*, *O. bacboensis*, *O. bolavensis*, *O. chapaensis*, *O. dulongensis*, *O. fengkaiensis*, *O. geminata*, *O. grahami*, *O. hainanensis*, *O. hejiangensis*, *O. huanggangensis*, *O. ishikawae*, *O. junlianensis*, *O. kuangwuensis*, *O. kweichowensis*, *O. lungshengensis*, *O. margaretae*, *O. mutschmanni*, *O. nanjiangensis*, *O. schmackeri*, *O. splendida*, *O. supranarina*, *O. tianmuii*, *O. tiannanensis*, *O. wuchuanensis*, *O. yizhangensis*, and *O. ichangensis* (*vs.* the presence of black bars).

By the absence of vocal sacs in males, *Odorrana liboensis* **sp. nov.** differs from *O. absita*, *O. amamiensis*, *O. andersonii*, *O. anlungensis*, *O. aureola*, *O. bacboensis*, *O. banaorum*, *O. bolavensis*, *O. cangyuanensis*, *O. chapaensis*, *O. chloronota*, *O. dulongensis*, *O. exiliversabilis*, *O. fengkaiensis*, *O. geminata*, *O. gigatympana*, *O. grahami*, *O. graminea*, *O. hainanensis*, *O. hejiangensis*, *O. huanggangensis*, *O. indeprensa*, *O. ishikawae*, *O. jingdongensis*, *O. junlianensis*, *O. khalam*, *O. kweichowensis*, *O. lungshengensis*, *O. macrotympana*, *O. morafkai*, *O. nanjiangensis*, *O. nasica*, *O. nasuta*, *O. orba*, *O. sinica*, *O. swinhoana*, *O. tianmuii*, *O. tiannanensis*, *O. tormota*, *O. trankieni*, *O. utsunomiyaorum*, *O. versabilis*, *O. yentuensis*, *O. yizhangensis*, *O. ichangensis*, and *O. zhaoi* (*vs.* the presence of vocal sacs).

By the relative lengths of fingers I<II<IV<III, *Odorrana liboensis* **sp. nov.** differs from *O. lipuensis* and *O. dulongensis* (*vs.* I=II<IV<III), from *O. absita*, *O. amamiensis*, and *O. anlungensis*(*vs.* II<I=IV<III), from *O. andersonii* (*vs.* I<II=IV<III), from *O. aureola*, *O. bacboensis*, *O. banaorum*, *O. bolavensis*, *O. chloronota*, *O. fengkaiensis*, *O. gigatympana*, *O. grahami*, *O. jingdongensis*, *O. junlianensis*, *O. kweichowensis*, *O. margaretae*, *O. mutschmanni*, *O. orba*, *O. schmackeri*, *O. swinhoana*, *O. tiannanensis*, *O. wuchuanensis*, and *O. yentuensis* (*vs.* II<I<IV<III), from *O. cangyuanensis* (*vs.* I<IV<II<III), from *O. exiliversabilis*, *O. hainanensis*, *O. hejiangensis*, *O. kuangwuensis*, *O. nasica*, *O. nasuta*, and *O. versabilis* (*vs.* II<IV<I<III), from *O. huanggangensis* (*vs.* I≤II=IV<III), from *O. splendida*, *O. supranarina*, and *O. trankieni* (*vs.* IV<II<I<III), from *O. zhaoi* (*vs.* I=IV<II<III).

By lacking white pectoral spinules in mature males, *Odorrana liboensis* **sp. nov.** differs from *O. andersonii*, *O. fengkaiensis*, *O. grahami*, *O. graminea*, *O. hainanensis*, *O. huanggangensis*, *O. jingdongensis*, *O. junlianensis*, *O. kweichowensis*, *O. lungshengensis*, *O. margaretae*, *O. tianmuii*, *O. yizhangensis*, and *O. zhaoi* (*vs.* presence of white pectoral spinules).

By having two metacarpal tubercles on the base of the hand, *Odorrana liboensis* **sp. nov.** differs from *O. absita*, *O. aureola*, and *O. bacboensis* (*vs.* lacking metacarpal tubercles), from *O. cangyuanensis*, *O. dulongensis*, *O. lungshengensis*, *O. nanjiangensis*, *O. orba*, *O. schmackeri*, *O. tiannanensis*, and *O. yizhangensis* (*vs.* one metacarpal tubercle), from *O. andersonii*, *O. exiliversabilis*, *O. fengkaiensis*, *O. hainanensis*, *O. hejiangensis*, *O. huanggangensis*, *O. jingdongensis*, *O. junlianensis*, *O. nasica*, *O. nasuta*, *O. tianmuii*, *O. tormota*, and *O. ichangensis* (*vs.* three metacarpal tubercles).

By having one metacarpal tubercle on the base of the metatarsus, *Odorrana liboensis* **sp. nov.** differs from *O. absita*, *O. amamiensis*, *O. exiliversabilis*, *O. nasica*, and *O. nasuta* (*vs.* two metatarsal tubercles).

The congeners *O. kweichowensis* and *O. wuchuanensis* have a sympatric distribution with *Odorrana liboensis* **sp. nov.** The new species can be distinguished from these species by a series of morphological characters as follows. The new species differs from *O. kweichowensis* by having a larger body size (adult males with a length of 47.1–49.9 mm *vs.* adult *O. kweichowensis* males with a length of 36.2–43.3 mm) and having a lower ratio of IND/IOD at 0.89 in males and 0.81 in females (*vs.* 1.14 in males and 1.19 in females for *O. kweichowensis*), lacks black bars on the lips (*vs.* the presence of black bars), an absence of vocal sacs in males (*vs.* the presence of vocal sacks), lacks large black spots on the dorsum (*vs.* large black spots in the center of the dorsum), has thighs with four brown bands and tibias with three (*vs.* thighs with five brown bands and tibias with six), lacks white pectoral spinules in mature males (*vs.* the presence of white pectoral spinules), and lacks toes with entire webbing (*vs.* full webbing).

The new species differs from *O. wuchuanensis* by having a smaller body size (SVL 47.1–49.9 mm in adult males and 55.8–58.2 mm in adult females *vs.* 71.1–76.5 mm in adult males and 75.8–90.0 mm in adult females) and a lower ratio of IND/IOD 0.89 in males and 0.81 in females (*vs.* 1.63 in males and 1.14

in females in *O. wuchuanensis*). The new species has a tibiotarsal articulation reaching to between the eye and the nostril when the leg is stretched forward (*vs.* reaching the nostril), lacks black bars on the lips (*vs.* the presence of black bars), lacks large black spots on the ventral surface (*vs.* the presence of large black spots), has relative finger lengths of I<II<IV<III (*vs.* II<I<IV<III), lacks black spots on the dorsum and ventral surfaces (*vs.* having large black spots in the dorsum and ventral surfaces), and features males without white spines on the dorsal surface of the arm (*vs.* the presence of large white spines).

Odorrana liboensis **sp. nov.** is phylogenetically closest to *O. lipuensis*, and this new species could be distinguished from the latter by tibiotarsal articulation reaching to between the eye and the nostril when the leg is stretched forward (*vs.* reaching the anterior corner of the eye); relative finger lengths I<II<IV<III (*vs.* I=II<IV<III); males and females with a lower ratio of TD/ED (mean 0.89 *vs. O. lipuensis*, mean 1.15); males and females with a higher ratio of IOD/HDW (in males 0.31–0.47, mean 0.40, and in females 0.39–0.41, mean 0.40 *vs.* in males 0.24–0.31, mean 0.27, and in females 0.23–0.31, mean 0.27); males with a higher ratio of TED/HDL (0.11–0.13, mean 0.12 *vs.* 0.08–0.10, mean 0.09); the absence of small white spiny grains from the anterior corner of the eye along the eye and via the tympanic membrane below to the anterior part of the cloacal foramen (*vs.* the presence of grains); indistinct brownish-black bands on limbs (*vs.* distinct); the throat, chest, and abdomen lacking black spots (*vs.* the presence of black spots); and the ventral surface of the limbs is pink (*vs.* light purple).

Distribution and ecology. *Odorrana liboensis* **sp. nov.** is known only from the type locality, Maolan National Nature Reserve, Libo County, Guizhou Province, China, at elevations between 645 and 728 m. The new species has only been found in one cave in the area located far from the village. There is no light in the cave, and the new species was found in a small pool approximately 1.5 m wide and 79 cm deep, about 145 m from the entrance of the cave, where the water temperature is approximately 20 ℃ all year round. The tadpoles were collected on July 23, 2016, but no pairs of male and female adults were found to hold them, and with four years of survey data, the adults were collected only from mid-July to mid-August. Therefore, we speculate that the breeding period begins in late June and continues until about mid-August. Inside this cave, *Odorrana liboensis* **sp. nov.** is sympatric with *Chinapotamon maolanense*, *Sinocyclocheilus longibarbatus*, *Hipposideros armiger*, *Aselliscus stoliczkanus*, *Murina liboensis*, and *Leopoldamys edwardsi*. Outside the cave, no adults and tadpoles of the new species were found during a herpetological survey in the vicinity. However, a number of amphibians and reptiles can be found outside the cave, including *Tylototriton asperrimus*, *Quasipaa boulengeri*, *Bufo gargarizans*, *Kurixalus eiffingeri*, *Rhacophorus dennysi*, *Goniurosaurus liboensis*, *Sinomicrurus macclellandi*, *Lycodon flavozonatum*, and *Orthriophis moellendorffi*.

4. Discussion

Most species of *Odorrana* live in montane streams. Previously, only two species (*O. wuchuanensis* and *O. lipuensis*) had been reported to live in cave environments (Fei *et al.*, 2012; Mo *et al.*, 2015). We discovered, and report on, a third species of *Odorrana*, *Odorrana liboensis* **sp. nov.**, that inhabits cave environments. Two of these species (including *O. wuchuanensis*) are found in karst caves in Guizhou. Phylogenetic analyses based on three mitochondrial genes suggested that *Odorrana liboensis* **sp. nov.** belongs to *Odorrana* but is distinct from its congeners. The genetic distances of 12S rRNA and 16S rRNA between the *Odorrana liboensis* **sp. nov.** and the closely related *O. lipuensis* were 6.06% and 5.19%. The genetic distances of 16S rRNA was greater than 5%, and this is greater than the distance that typically represents differentiation, at the species level, in frogs (>3%) (Vences *et al.*, 2005; Fouquet *et al.*, 2007). The new species was different from its congeners on the basis of many morphological characters, and this supports its validity. *Odorrana liboensis* **sp. nov.** described here increases the number of *Odorrana* species to 62, with 39 recorded from China (Frost, 2021; AmphibiaChina, 2021).

Based on 49 previously named species, one new species, and three mitochondrial genes, we conducted a phylogenetic study of the genus *Odorrana*. The number of species covered here and the amount of data analyzed exceeds previously reported data (Chen *et al.*, 2013; Li *et al.*, 2018a). Eight highly supported major clades were identified in *Odorrana* (Clades A–H). The topology of this tree differed significantly from previous studies, focusing mainly on the root evolutionary branches of *Odorrana* (Figure 2). In the phylogenetic tree, *O. lipuensis* + *Odorrana liboensis* **sp. nov.** was the first species to diverge from the genus *Odorrana*, whereas in other studies by Chen *et al.* (2013) and Li *et al.* (2018a), the first species to diverge was *O. chapaensis*. In our phylogenetic tree, *O. chapaensis* + O. *geminata* (Clade D1) serves as a sister taxonomic unit to Clade D2 consisting of *O. andersonii* as well as *O. wuchuanensis*, *O. mutschmanni*, *O. yizhangensis*, *O. lungshengensis*, and *O. anlungensis*. In contrast, in previous studies, *O. chapaensis* appeared as a sister taxon in a clade that included all other *Odorrana* (Chen *et al.*, 2013; Li *et al.*, 2018a), or as a sister taxon to *Odorrana* other than *O. lipuensis* (He, 2017). Ye and Fei (2001) suggested that the primitive taxa of *Odorrana* may have originated from the Hengduan Mountains and the plateau of western Yunnan. The Guizhou plateau may have been the center of differentiation of *Odorrana* (Ye and Fei, 2001). *O. lipuensis* and *Odorrana liboensis* **sp. nov.** appear to have diverged from *Odorrana* and formed the ancestral evolutionary branch of the genus *Odorrana*. Therefore, we believe that the ancestral distribution

of *Odorrana* may be the region south of Guizhou and northwest of Guangxi. However, this preliminary speculation needs to be supported by data from additional species and nuclear genes.

Biodiversity conservation in southwestern China is a priority of the Chinese government (Ministry of Environmental Protection, 2015). Biodiversity conservation programs in this region play an important role in maintaining the stability of mountain ecosystems as well as protecting biodiversity. In the past three years alone, 16 new amphibian species have been described from Guizhou Province, China (Zhang *et al*., 2017; Li *et al*., 2018a, b; Li *et al*., 2019a, b; Li *et al*., 2020a, b; Lyu *et al*., 2019; Wang *et al*., 2019; Luo *et al*., 2020; Liu *et al*., 2020; Lyu *et al*., 2020; Su *et al*., 2020; Wei *et al*., 2020; Wang *et al*., 2020; Cheng *et al*., 2021). The discovery of these new species suggests that amphibian species diversity in this region is severely underestimated. In the context of global warming, there is an urgent need for a comprehensive, systematic, and in-depth survey of the impacts of climate change on terrestrial vertebrates to provide a basis for scientific decisions regarding amphibian conservation (IPCC, 2014).

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Appendix

Specimens examined

Odorrana lipuensis (*n* = 8): China: Guangxi: Lipu County (type locality): four males: NHMG 1306001, NHMG 1306002, NHMG 20140702, and NHMG 20140703; four females: NHMG 1303019, NHMG 1303018, NHMG 1306003, and NHMG 20140701.

Odorrana kweichowensis (*n* = 35): China: Guizhou Province: Jinsha County (type locality). 18 males: GZNU 20170717008–010, GZNU 20170717014, GZNU 20170717016–019, GZNU 20170717021–023, GZNU 20170717025, GZNU 20170717026, GZNU 20170717028–7030, GZNU 20170718003, and GZNU 2017071800; 17 females: GZNU 20170717001–007, GZNU 20170718001–002, GZNU 20170725001–007, and GZNU 20170725013.

Odorrana wuchuanensis (*n* = 17): China: Guizhou Province: Libo County (topotype locality): 12 males: GZNU 20160729001–006, GZNU 20160729008, GZNU 20160806001–005; five females: GZNU 20160729007, GZNU 20160809001, GZNU 20160809003, GZNU 20160809006, and GZNU 20160809011.