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A new *Leptobrachella* species (Anura, Megophryidae) from South China, with comments on the taxonomic status of *L. chishuiensis* and *L. purpurus*

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Abstract

A new species of Leaf Litter Toad, *Leptobrachella shimentaina* **sp. nov.**, is described from the Shimentai and Luokeng nature reserves of northern Guangdong Province, southern China. The new taxon can be distinguished from all recognized congeners by a combination of discrete morphological character state differences relating to its small body size (SVL 26.4–28.9 mm in six adult males, 30.1 and 30.7 mm in two adult females); a number of apparently fixed color pattern character differences (including eye coloration and color pattern features from dorsal, ventral, and dorsolateral surfaces of its head, body, limbs, and ventrum); the morphological and discrete characteristics of the external phenotype (the skin texture of dorsum and ventrum, the presence of supra-axillary and ventrolateral glands, the wide dermal fringes and rudimentary webbing on toes, and the uninterrupted longitudinal ridges under toes). Two samples of this new species previously were proposed as representing a new, unnamed species. We now substantiate this claim by providing diagnostic comparisons of discrete character differences. In addition, we also discuss taxonomic uncertainty surrounding the identity of two congeners, *L. chishuiensis* and *L. purpurus*, which we interpret as indicative of taxonomic inflation in the species-rich subfamily Megophryidae.

Key Words

Leptobrachella shimentaina sp. nov., *L. chishuiensis*, *L. purpurus*, morphology, taxonomy

Introduction

The genus *Leptobrachella* Smith, 1925 recently was found to be paraphyletic with *Leptolalax* Dubois, 1983 based on a comprehensive molecular analysis combining fragments of mitochondrial and nuclear DNA markers by Chen et al. (2018). They suggested to synonymize two genera on account of their results clearly nested *Leptobrachella* within *Leptolalax*, though the type species *Leptobrachella mjobergi* Smith, 1925 was not included. With 92 species, the forest-dependent genus *Leptobrachella* is widely distributed in southern China, Myanmar, northeastern India, Indochina region, Borneo and Natuna Island (Frost 2022). Species diversity in *Leptobrachella* may be underestimated, as suggested by 15 undescribed species proposed by Chen et al. (2018).

One of the most widely-distributed species, *Leptobrachella liui* (Fei & Ye, 1990) has been reported from Fujian, Guangdong, Guizhou, Hunan, and Zhejiang, provinces, Guangxi Zhuang Autonomous Region, and Hong Kong

SAR, China (Fei and Ye 1992; Fei et al. 2009; Fei et al. 2012). Later, Li et al. (2011) recognized *Leptobrachella* populations from Hong Kong and Guangdong (Xinyi City, Fengkai County, Shenzhen City) as the species *L. pelodytoides* (Boulenger, 1893). However, more recently, populations in Shenzhen of Guangdong and Hong Kong have been proposed as another species, *L. laui* (Sung, Yang & Wang, 2014), and those in Xinyi have been described as *L. yunkaiensis* Wang, Li, Lyu & Wang, 2018. Although the taxonomic status of the population from Fengkai, western Guangdong remained unresolved due to the lack of molecular data, another noteworthy lineage from Shimentai Nature Reserve, northern Guangdong was indicated by Chen et al. (2018), as a putatively undescribed species ("*Leptobrachella* sp. 6").

In this paper we evaluate discrete character state differences and phylogenetic relationships of seven additional specimens from Shimentai Nature Reserve and a single specimen from the adjacent Luokeng Nature Reserve (northern Guangdong, southern China Fig. 1), which substantiate the recognition of "*Leptobrachella* sp. 6" (Chen et al. 2018) as a distinctive new species.

Material and methods

Phylogenetic analyses

Eighteen new individuals were sequenced for phylogenetic analyses, and 71 sequences were obtained from GenBank (Suppl. material 1: Table S1). Our sampling includes individuals from most recognized congeners from China and neighboring countries. The 16S ribosomal RNA mitochondrial gene (16S rRNA) fragment was sequenced for new samples; DNA extraction, PCR, and sequencing follow Wang et al. (2020).

Sequences were aligned with Clustal X 2.0 (Thompson et al. 1997) with default parameters. For GenBank sequences missing intervening sequence segments, we filled blank nucleotide positons "N" to indicate missing data. The aligned data was trimmed using default parameters and allowing no gap positions in Gblocks version 0.91b (Castresana 2000). We ran Jmodeltest v2.1.2 (Darriba et al. 2012; with Akaike and Bayesian information criteria) on our alignment and obtained the best-fitting nucleotide substitution model of GTR + I + G (General Time Reversible model, with variable sites modelled according to the Gamma distribution, and a portion of the sites invariant). Phylogenetic analysis was conducted using Bayesian inference (BI) in MrBayes 3.2.4 (Ronquist et al. 2012) and maximum likelihood (ML) in maximum likelihood (ML) in Randomized Axelerated Maximum Likelihood (RAxML, Stamatakis 2006) with RAxML GUI 1.3 (Silvestro and Michalak 2012). For the ML analysis, an optimal tree was obtained and branch supports were evaluated with 1000 rapid bootstrapping replicates. For the BI analysis, two independent runs with four Markov Chain Monte Carlo simulations were performed for ten million iterations and sampled every 1000 iterations. The first 25% of the samples were discarded as burn-in, leaving 7500 samples

Figure 1. Localities of *Leptobrachella shimentaina* sp. nov. (samples ID 1–10, Shimentai Nature Reserve, Guangdong, China; sample ID 11, Luokeng Nature Reserve, Guangdong, China); *Leptobrachella bijie* (samples ID 38–40, Zhaozishan Nature Reserve, Guizhou, China; sample ID 41, Chishui, Guizhou, China; samples ID 42–43, Huagaoxi Nature Reserve, Guizhou, China); *Leptobrachella chishuiensis* (samples ID 44–46, Chishui, Guizhou, China); *Leptobrachella alpina* (samples ID 50–51, Mt Huangcaoling, Yunnan, China; sample ID 52, Pu'er, Yunnan, China); and *Leptobrachella purpurus* (samples ID 53–54, Yingjiang, Yunnan, China). Numbers correspond to the ID numbers in Suppl. material 1: Table S1.

in the final summary. Convergence of the Markov Chain Monte Carlo simulations was assessed by PSRF < 0.01 and ESS (effective sample size) value > 200 using Tracer 1.4 (http://tree.bio.ed.ac.uk/software/tracer/). Nodes having ML bootstrap values (BS) ≥ 70 and BI posterior probabilities (BPP) ≥ 0.95 were considered well supported.

Morphology

Our specimens of the putatively unnamed species were collected during opportunistic night searches. All specimens were euthanized, fixed in 5% buffered formalin for five hours, and then preserved in 70% ethanol, and subsequently deposited in The Museum of Biology, Sun Yat-sen University (SYS) and Chengdu Institute of Biology, Chinese Academy of Sciences (CIB), China.

Following Fei et al. (2009) and Rowley et al. (2013), measurements were taken with digital calipers (Neiko 01407A Stainless Steel 6-Inch Digital Calipers) to the nearest 0.1 mm. Measurements include: snout-vent length (SVL) from the tip of the snout to posterior margin of the vent; head length (HDL) from the tip of the snout to the articulation of the jaw; head width (HDW) at the commissure of the jaws; snout length (SNT) from the tip of the snout to the anterior corner of the eye; eye diameter (EYE) from the anterior corner of the eye to posterior corner of the eye; internasal distance (IND); interorbital distance (IOD); horizontal diameter of tympanum (TMP); tympanum-eye distance (TEY) from the anterior edge of tympanum to posterior corner of the eye; tibial length (TIB) from the outer surface of the flexed knee to the heel; manus length (ML) from the tip of the third finger to the proximal edge of inner palmar tubercle; pes length (PE) from the tip of the fourth toe to the proximal edge of the inner metatarsal tubercle; length of lower arm and hand (LAHL) from the tip of the third finger to elbow; and hindlimb length (HLL) from the tip of the fourth toe to vent.

Sex was determined by direct observation of calling in life, the presence of internal vocal sac openings (males), or the presence of eggs, seen via external inspection of the abdomen (females). Comparative morphological data for other congeneric species of *Leptobrachella* were obtained from museum specimens (Appendix 1) and from the literature (Table 1).

Table 1. Data source of the currently known species of the genus *Leptobrachella*.

ID	*Leptobrachella* species	Literature obtained
1	*L. aerea* (Rowley, Stuart, Richards, Phimmachak & Sivongxay, 2010c)	Rowley et al. 2010c
2	*L. aspera* Wang, Lyu, Qi & Wang, 2020	Wang et al. 2020
3	*L. alpina* (Fei, Ye & Li, 1990)	Fei et al. 1990; Fei et al. 2009, 2016
4	*L. applebyi* (Rowley & Cao, 2009)	Rowley and Cao 2009
5	*L. arayai* (Matsui, 1997)	Matsui 1997
6	*L. ardens* (Rowley, Tran, Le, Dau, Peloso, Nguyen, Hoang, Nguyen & Ziegler, 2016)	Rowley et al. 2016
7	*L. baluensis* Smith, 1931	Dring 1983; Eto et al. 2016
8	*L. bashaensis* Lyu, Dai, Wei, He, Yuan, Shi, Zhou, Ran, Kuang, Guo, Wei & Yuan, 2020	Lyu et al. 2020a
9	*L. bijie* Wang, Li, Li, Chen & Wang, 2019	Wang et al. 2019
10	*L. bidoupensis* (Rowley, Le, Tran & Hoang, 2011)	Rowley et al. 2011
11	*L. bondangensis* Eto, Matsui, Hamidy, Munir & Iskandar, 2018	Eto et al. 2018
12	*L. botsfordi* (Rowley, Dau & Nguyen, 2013)	Rowley et al. 2013
13	*L. bourreti* (Dubois, 1983)	Ohler et al. 2011
14	*L. brevicrus* Dring, 1983	Dring 1983; Eto et al. 2015
15	*L. crocea* (Rowley, Hoang, Le, Dau & Cao, 2010)	Rowley et al. 2010a
16	*L. chishuiensis* Li, Liu, Wei & Wang, 2020	Li et al. 2020
17	*L. damingshanensis* Chen, Yu, Cheng, Meng, Wei, Zhou & Lu, 2021	Chen et al. 2021b
18	*L. dorsospina* Wang, Lyu, Qi & Wang, 2020	Wang et al. 2020
19	*L. dringi* (Dubois, 1987)	Inger et al. 1995; Matsui and Dehling 2012
20	*L. eos* (Ohler, Wollenberg, Grosjean, Hendrix, Vences, Ziegler & Dubois, 2011)	Ohler et al. 2011
21	*L. feii* Chen, Yuan & Che, 2020	Chen et al. 2020
22	*L. firthi* (Rowley, Hoang, Dau, Le & Cao, 2012)	Rowley et al. 2012
23	*L. fritinniens* (Dehling & Matsui, 2013)	Dehling and Matsui 2013
24	*L. fuliginosa* (Matsui, 2006)	Matsui 2006
25	*L. flaviglandulosa* Chen, Wang & Che, 2020	Chen et al. 2020
26	*L. fusca* Eto, Matsui, Hamidy, Munir & Iskandar, 2018	Eto et al. 2018
27	*L. gracilis* (Günther, 1872)	Günther 1872; Dehling 2012b
28	*L. hamidi* (Matsui, 1997)	Matsui 1997
29	*L. graminicola* Nguyen, Tapley, Nguyen, Luong & Rowley, 2021	Nguyen et al. 2021
30	*L. heteropus* (Boulenger, 1900)	Boulenger 1900
31	*L. isos* (Rowley, Stuart, Neang, Hoang, Dau, Nguyen & Emmett, 2015)	Rowley et al. 2015a
32	*L. itiokai* Eto, Matsui & Nishikawa, 2016	Eto et al. 2016
33	*L. juliandringi* Eto, Matsui & Nishikawa, 2015	Eto et al. 2015
34	*L. jinshaensis* Cheng, Shi, Li, Liu, Li & Wang, 2021	Cheng et al. 2021
35	*L. kajangensis* (Grismer, Grismer & Youmans, 2004)	Grismer et al. 2004
36	*L. kalonensis* (Rowley, Tran, Le, Dau, Peloso, Nguyen, Hoang, Nguyen & Ziegler, 2016)	Rowley et al. 2016

ID	*Leptobrachella* species	Literature obtained
37	*L. kecil* (Matsui, Belabut, Ahmad & Yong, 2009)	Matsui et al. 2009
38	*L. khasiorum* (Das, Tron, Rangad & Hooroo, 2010)	Das et al. 2010
39	*L. lateralis* (Anderson, 1871)	Anderson 1871; Humtsoe et al. 2008
40	*L. laui* (Sung, Yang & Wang, 2014)	Sung et al. 2014
41	*L. liui* (Fei & Ye, 1990)	Fei et al. 1990; Fei et al. 2009; Sung et al. 2014; this study
42	*L. macrops* (Duong, Do, Ngo, Nguyen & Poyarkov, 2018)	Duong et al. 2018
43	*L. maculosa* (Rowley, Tran, Le, Dau, Peloso, Nguyen, Hoang, Nguyen & Ziegler, 2016)	Rowley et al. 2016
44	*L. mangshanensis* (Hou, Zhang, Hu, Li, Shi, Chen, Mo & Wang, 2018)	Hou et al. 2018; this study
45	*L. maoershanensis* (Yuan, Sun, Chen, Rowley & Che, 2017)	Yuan et al. 2017
46	*L. marmorata* (Matsui, Zainudin & Nishikawa, 2014b)	Matsui et al. 2014b
47	*L. maura* (Inger, Lakim, Biun & Yambun, 1997)	Inger et al. 1997
48	*L. melanoleuca* (Matsui, 2006)	Matsui 2006
49	*L. melica* (Rowley, Stuart, Neang & Emmett, 2010)	Rowley et al. 2010b
50	*L. minima* (Taylor, 1962)	Taylor 1962; Ohler et al. 2011
51	*L. mjobergi* Smith, 1925	Eto et al. 2015
52	*L. murphyi* Chen, Suwannapoom, Wu, Poyarkov, Xu, Pawangkhanant & Che, 2021	Chen et al. 2021a
53	*L. nahangensis* (Lathrop, Murphy, Orlov & Ho, 1998)	Lathrop et al. 1998
54	*L. natunae* (Günther, 1895)	Günther 1895
55	*L. namdongensis* Hoang, Nguyen, Luu, Nguyen & Jiang, 2019	Hoang et al. 2019
56	*L. neangi* Stuart & Rowley, 2020	Stuart and Rowley 2020
57	*L. niveimontis* Chen, Poyarkov, Yuan & Che, 2020	Chen et al. 2020
58	*L. nokrekensis* (Mathew & Sen, 2010)	Mathew and Sen 2010
59	*L. nyx* (Ohler, Wollenberg, Grosjean, Hendrix, Vences, Ziegler & Dubois, 2011)	Ohler et al. 2011
60	*L. oshanensis* (Liu, 1950)	Liu, 1950; Shi et al. 2021
61	*L. pallida* (Rowley, Tran, Le, Dau, Peloso, Nguyen, Hoang, Nguyen & Ziegler, 2016)	Rowley et al. 2016
62	*L. palmata* Inger & Stuebing, 1992	Inger and Stuebing 1992
63	*L. parva* Dring, 1983	Dring 1983
64	*L. pelodytoides* (Boulenger, 1893)	Boulenger 1893; Ohler et al. 2011
65	*L. petrops* (Rowley, Dau, Hoang, Le, Cutajar & Nguyen, 2017)	Rowley et al. 2017a
66	*L. picta* (Malkmus, 1992)	Malkmus 1992
67	*L. platycephala* (Dehling, 2012)	Dehling 2012a
68	*L. pluvialis* (Ohler, Marquis, Swan & Grosjean, 2000)	Ohler et al. 2000, 2011
69	*L. puhoatensis* (Rowley, Dau & Cao, 2017)	Rowley et al. 2017b
70	*L. purpurus* (Yang, Zeng & Wang, 2018)	Yang et al. 2018
71	*L. purpuraventra* Wang, Li, Li, Chen & Wang, 2019	Wang et al. 2019
72	*L. pyrrhops* (Poyarkov, Rowley, Gogoleva, Vassilieva, Galoyan & Orlov, 2015)	Poyarkov et al. 2015
73	*L. rowleyae* (Nguyen, Poyarkov, Le, Vo, Ninh, Duong, Murphy & Sang, 2018)	Nguyen et al. 2018
74	*L. sabahmontana* (Matsui, Nishikawa & Yambun, 2014)	Matsui et al. 2014a
75	*L. serasanae* Dring, 1983	Dring 1983
76	*L. shangsiensis* Chen, Liao, Zhou & Mo, 2019	Chen et al. 2019
77	*L. sola* (Matsui, 2006)	Matsui 2006
78	*L. suiyangensis* Luo, Xiao, Gao & Zhou, 2020	Luo et al. 2020
79	*L. sungi* (Lathrop, Murphy, Orlov & Ho, 1998)	Lathrop et al. 1998
80	*L. shiwandashanensis* Chen, Peng, Pan, Liao, Liu & Huang, 2021	Chen et al. 2021c
81	*L. tadungensis* (Rowley, Tran, Le, Dau, Peloso, Nguyen, Hoang, Nguyen & Ziegler, 2016)	Rowley et al. 2016
82	*L. tamdil* (Sengupta, Sailo, Lalremsanga, Das & Das, 2010)	Sengupta et al. 2010
83	*L. tengchongensis* (Yang, Wang, Chen & Rao, 2016)	Yang et al. 2016
84	*L. tuberosa* (Inger, Orlov & Darevsky, 1999)	Inger et al. 1999
85	*L. ventripunctata* (Fei, Ye & Li, 1990)	Fei et al. 1990; Fei et al. 2009, 2016
86	*L. wuhuangmontis* Wang, Yang & Wang, 2018	Wang et al. 2018
87	*L. wulingensis* Qian, Xia, Cao, Xiao & Yang, 2020	Qian et al. 2020
89	*L. yingjiangensis* (Yang, Zeng & Wang, 2018)	Yang et al. 2018
90	*L. yunkaiensis* Wang, Li, Lyu & Wang, 2018	Wang et al. 2018
91	*L. yeae* Shi, Hou, Song, Jiang & Wang, 2021	Shi et al. 2021
92	*L. zhangyapingi* (Jiang, Yan, Suwannapoom, Chomdej & Che, 2013)	Jiang et al. 2013

Results

Essentially identical topologies were obtained by our ML and BI analyses (Fig. 2). In both phylogenetic estimates, all *Leptobrachella* samples formed a strongly-supported monophyletic clade. All *Leptobrachella* samples from populations from Shimentai and Luokeng nature reserves form a monophyletic clade, without structure of within-population genetic divergence and with strong support (BPP = 1.00, BS = 100). The Shimentai and Luokeng lineage represents an independent lineage within *Leptobrachella*, relatively close to the lineages of *L. liui*, *L. mangshanensis*, *L. maoershanensis*, *L. bashaensis*, *L. laui*, and *L. yunkaiensis*. Nevertheless, support for the large clade

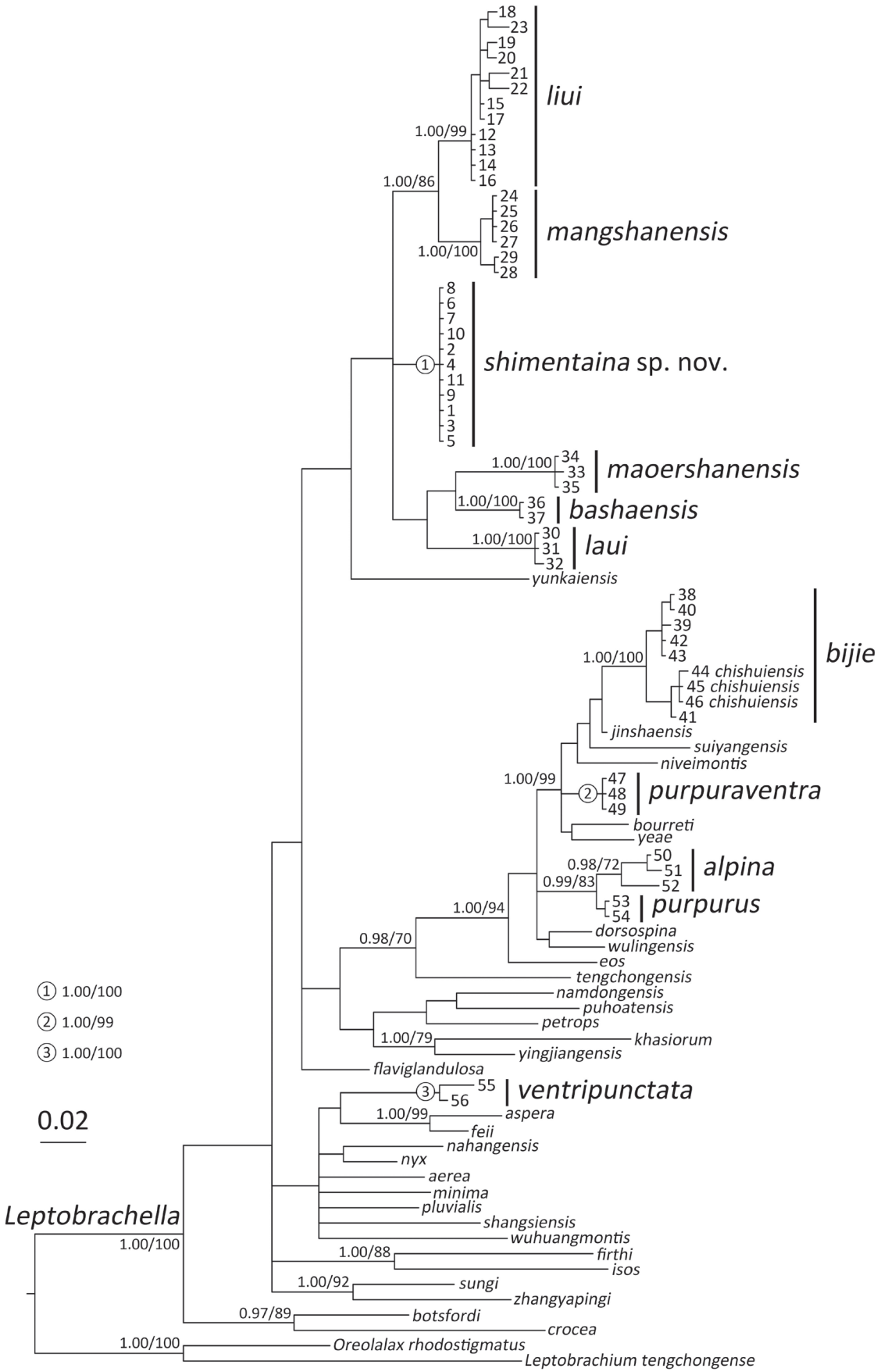

Figure 2. Bayesian inference tree derived from partial DNA sequences of the mitochondrial 16S r RNA gene. Numbers before slashes indicate Bayesian posterior probabilities and numbers after slashes are bootstrap support for maximum likelihood (1000 replicates) analyses. The number at the branch terminal corresponds to the ID in Suppl. material 1: Table S1.

including these species is insignificant, therefore, the relationships among these species are still unresolved. Detailed morphological examination has revealed discrete, diagnostic (non-overlapping ranges in traditional characters) differences among the specimens from this unnamed lineage and all other congeners. Our phylogenetic result and morphological comparison unanimously agree with the proposal that the Shimentai and Luokeng lineage represents an undescribed new species, i.e. "*Leptobrachella* sp. 6" in Chen et al. (2018). Therefore, based on the discrete and diagnostic morphological character differences, *Leptobrachella* populations from Shimentai and Luokeng nature reserves are described below as a new species.

Taxonomic account

Leptobrachella shimentaina **J. Wang, Z.-T. Lyu & Y.-Y. Wang, sp. nov.**

http://zoobank.org/CF6EEF64-F539-415B-AD11-FA19C56BC3D5

Shimentai Leaf Litter Toad (in English) / Shi Men Tai Zhang Tu Chan (石门台掌突蟾in Chinese)

Figs 3–6

Chresonymy. "*Leptolalax* sp.6" (Chen et al. 2018).

Type material. ***Holotype*** ♂. SYS a007684, from Jiuzhou Yizhan (24°23'38.01"N, 113°06'35.38"E; ca. 300 m a.s.l.), Shimentai Nature Reserve, Yingde City, Guangdong Province, China, collected by Jian Wang and Yong-You Zhao on 23 April 2019.

Paratypes (n = 7). 5 ♂: SYS a007683/CIB116079, same collection place as holotype; SYS a007685–7686, collected by Yu-Long Li and Hong-Hui Chen on 23 April 2019 from Shijiao (24°26'35.31"N, 113°09'21.55"E; ca 400 m a.s.l.), Shimentai Nature Reserve; SYS a007687, collected by Jian Wang and Yong-You Zhao on 24 April 2019 from Longtankeng (24°26'31.38"N, 113°15'28.81"E; ca 310 m a.s.l.), Shimentai Nature Reserve; SYS a008329, collected by Jian Wang on 27 April 2020 from Luokeng Nature Reserve (24°31'42.3"N, 113°15'54.3"E; ca 590 m a.s.l.), Shaoguan City, Guangdong Province, China. 2 ♀: SYS a004711–4712, collected by Ying-Yong Wang, Jian Wang, and Zhi-Tong Lyu on 27 April 2016 from Hengshitang (24°26'14.92"N, 113°17'50.48"E; ca 380 m a.s.l.), Shimentai Nature Reserve.

Etymology. The specific epithet "*shimentaina*" is an adjective derived from "shimentai", referring to the type locality of the new species, Shimentai Nature Reserve, "*ina*" is used as a feminine suffix which indicates the relationship of position.

Diagnosis. (1) small body size [SVL 26.4–28.9 mm in six adult males, SVL 30.1 and 30.7 mm in two adult females], (2) iris bicolored, upper half coppery orange and lower half silver, (3) tympanum distinct, (4) supratympanic line black, (5) fingers unwebbed, with distinct lateral fringes in males [absence in females], (6) toes with rudimentary webbing, lateral fringes wide in males [narrow in females], (7) longitudinal ridges under toes continuous, with constrictions at interphalangeal articulations, (8) heels slightly overlapping when adpressed, tibial-tarsal articulation reaching mid-orbit, (9) relative lengths of fingers I = II = IV < III, and toe I < II < III = V < IV, (10) dorsal surface shagreened and granular, lacking enlarged warts, with some granules forming short longitudinal folds, (11) dorsum grayish brown to yellowish brown, with small light orange granules and distinct darker brown scattered markings with irregular light orange pigmentation, (12) flanks with several dark spots, (13) ventral surface grayish pink, with distinct hazy brown speckling on chest and ventrolateral flanks, (14) densely-distributed, small, raised pectoral and abdominal tubercles present; (15) dorsal surfaces of forelimbs and digits with dark transverse bars.

Description of holotype. Adult male. Body size small, SVL in 28.6 mm. Head length slightly larger than head width, HDW/HDL 0.91; snout slightly protruding, projecting slightly beyond margin of lower jaw; nostril closer to snout than eye; canthus rostralis gently rounded; loreal region slightly concave; interorbital space flat, internarial distance larger than interorbital distance, IND/IOD 1.10; pineal ocellus absent; pupil vertical; snout longer than eye diameter, SNT/EYE 1.19; tympanum distinct, rounded, diameter smaller than that of eye and larger than tympanum-eye distance, TMP/EYE 0.41, TEY/TMP 0.48; upper margin of tympanum in contact with supratympanic ridge; vomerine teeth absent; a single vocal sac; vocal sac openings slit-like, paired, located posterolaterally on floor of mouth, close to margins of mandible; tongue deeply notched posteriorly; supratympanic ridge distinct, extending from posterior corner of eye to supra-axillary gland.

Tips of fingers rounded, slightly swollen; relative finger lengths I = II = IV < III; nuptial pad absent; subarticular tubercles absent; inner palmar tubercle large, rounded, distinctly separated from outer palmar tubercle; outer palmar tubercle small, rounded; fingers lacking interdigital webbing, with distinct lateral fringes. Tips of toes rounded, slightly swollen; relative toe length I < II < III = V < IV; longitudinal ridges under toes continuous, with constrictions at interphalangeal articulations; inner metatarsal tubercle large, oval; outer metatarsal tubercle absent; interdigital webbing between toes rudimentary; wide lateral fringes present on all toes. Tibia 47% of snout-vent length; tibiotarsal articulation reaches to middle of eye; heels slightly overlapping when thighs are appressed at right angles with respect to body.

Dorsal surface shagreened and granular, lacking enlarged tubercles or warts, some granules forming short longitudinal folds; ventral skin smooth, densely-distributed small raised scapular and abdominal tubercles present; pectoral and femoral glands oval; both larger in diameter than tip of fingers; femoral glands larger in diameter than tip of toes; femoral gland situated on posteroventral surface of thigh, closer to knee than to vent; supra-axillary gland raised. Ventrolateral gland distinctly visible, forming an longitudinal uncontinuous series.

Coloration of holotype in life. Dorsal background color yellowish-brown, with small orange granules, distinct dark brown markings, and rounded spots, and scattered

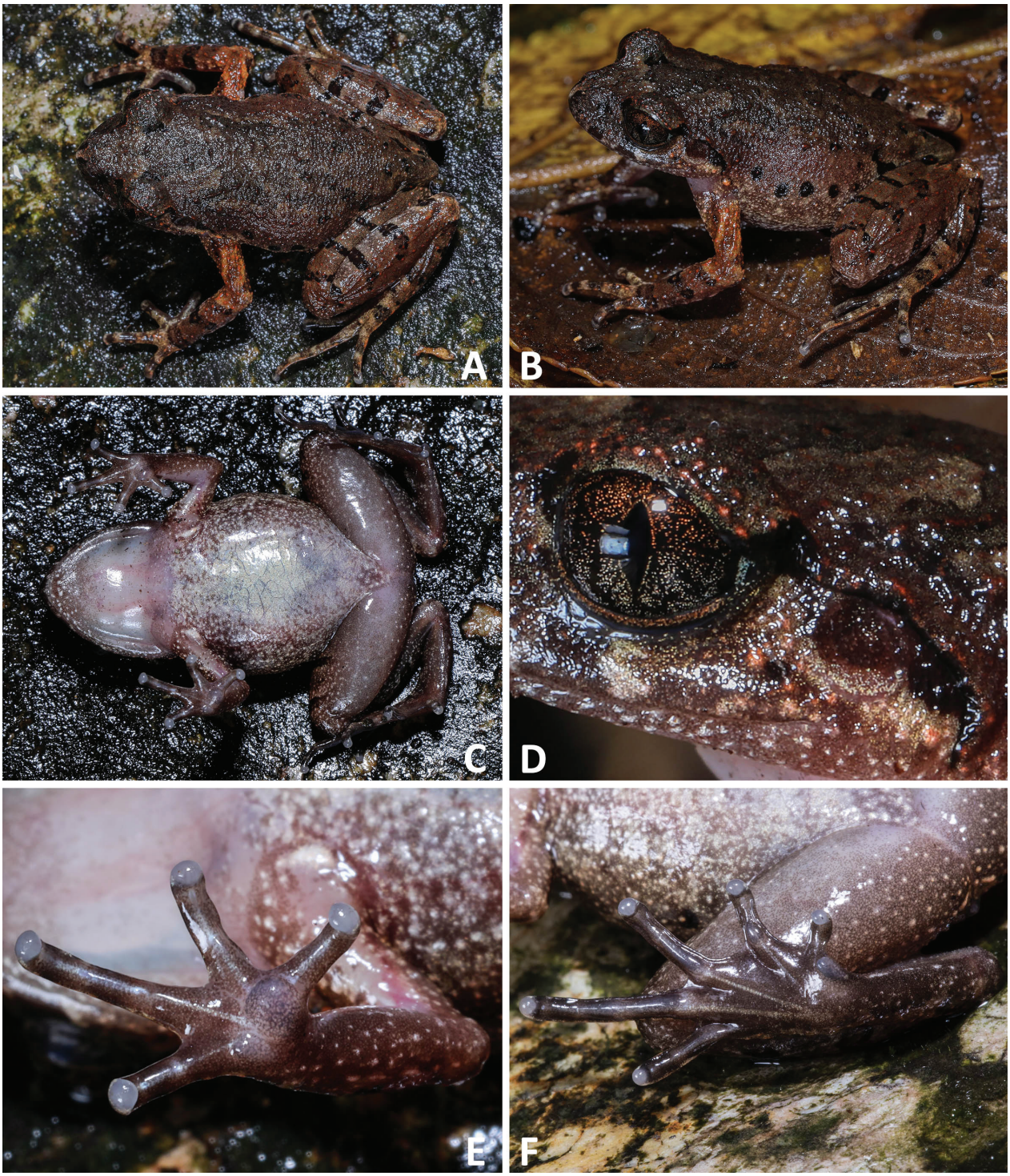

Figure 3. Morphological features of the holotype of *Leptobrachella shimentaina* sp. nov., SYS a007684 in life: **A.** Dorsal view; **B.** Dorsolateral view; **C.** Ventral view; **D.** Character of eye and temporal region; **E.** Ventral view of hand; **F.** Ventral view of foot.

with irregular light grayish-brown pigmentation. A dark brown inverted triangular marking present between anterior corners of eyes, connecting to dark brown W-shaped marking in interorbital region. This W-shaped marking is in connection to the other W-shaped marking on occipital region. Tympanum dark brown, lower margin grayish yellow. Supratympanic line black. Dorsal surfaces of body and limbs with small orange granules; a pair of dark brown vertical bars present under eyes; transverse dark brown bars on dorsal surfaces of distal limbs and digits; distinct dark brown blotches on flanks; surfaces of elbows and upper arms coppery orange, without dark bars.

Surface of throat, chest, and belly grayish pink, with distinct hazy brown speckling on chest and ventrolateral flanks, without black spots; surface of chin and lower lip brown with grayish white spots and patches; ventral surface of limbs brown with pink hues. Supra-axillary gland coppery orange, pectoral glands grayish white, femoral

Figure 4. The holotype of *Leptobrachella shimentaina* sp. nov., SYS a007684 in preservative.

glands coppery orange, ventrolateral glands brown. Iris bicolored, upper half coppery orange, lower half silver.

Coloration of holotype in preservative (Fig. 4). Dorsal background color grayish brown, scattered with irregular light grayish-brown pigmentation. All markings, bars and spots become more distinct. Tympanum dark brown, lower margin gray.

Ventral surface yellowish brown; speckling on chest and ventrolateral flanks become more distinct; ventral surface of limbs dark brown. Supra-axillary, pectoral, and ventrolateral glands greyish yellow.

Variation. Measurements and body proportions are listed in Table 2. All male paratypes from Shimentai Nature Reserve (SYS a007683/CIB116079, SYS a007685 (Fig. 5B), 7686 (Fig. 5C), 7687) show very similar morphological characters to holotype SYS a007684; paratype SYS a008329 (Fig. 6) from Luokeng Nature Reserve shows a darker coloration on dorsum, and brighter coloration on ventrum. Moreover, female paratypes, SYS a004711 (Fig. 5A) and SYS a004712 show lighter background coloration and more obvious dark brown marking orange tubercles on back.

Table 2. Measurements (minimum–maximum (mean ± SD); in mm), and body proportions of *Leptobrachella shimentaina* sp. nov.

Vocher	SYS a007683	SYS a007684	SYS a007685	SYS a007686	SYS a007687	SYS a008329	Range	Vocher	SYS a004711	SYS a004712	Range
Sex	Male	Male	Male	Male	Male	Male	Males (n = 6)	**Sex**	Female	Female	Females (n = 2)
SVL	28.9	28.6	28.4	28.7	28.4	26.4	26.4–28.9 (28.2 ± 0.9)	**SVL**	30.1	30.7	30.1–30.7 (30.4 ± 0.4)
HDL	11.7	10.7	10.8	10.9	10.8	9.8	9.8–11.7 (10.8 ± 0.6)	**HDL**	10.1	10.4	10.1–10.4 (10.3 ± 0.2)
HDW	9.7	9.7	9.7	9.7	9.7	9.2	9.2–9.7 (9.6 ± 0.2)	**HDW**	9.7	9.9	9.7–9.9 (9.8 ± 0.2)
SNT	4.3	4.2	4.1	4.3	4.2	3.3	3.3–4.3 (4.1 ± 0.4)	**SNT**	4.0	4.3	4.0–4.3 (4.1 ± 0.2)
IND	2.9	2.7	2.9	2.8	2.7	2.9	2.7–2.9 (2.8 ± 0.1)	**IND**	2.7	2.8	2.7–2.8 (2.7 ± 0.1)
IOD	2.6	2.5	2.5	2.5	2.5	2.6	2.5–2.6 (2.5 ± 0.1)	**IOD**	2.7	2.8	2.7–2.8 (2.7 ± 0.0)
EYE	3.5	3.5	3.4	3.4	3.4	3.3	3.3–3.5 (3.4 ± 0.1)	**EYE**	3.5	3.6	3.5–3.6 (3.5 ± 0.1)
TMP	1.5	1.5	1.5	1.5	1.5	1.5	1.5–1.5 (1.5 ± 0.0)	**TMP**	1.5	1.8	1.5–1.8 (1.7 ± 0.2)
TEY	0.7	0.7	0.7	0.7	0.7	0.6	0.6–0.7 (0.7 ± 0.0)	**TEY**	0.6	0.9	0.6–0.9 (0.8 ± 0.2)
ML	7.4	7.2	7.2	7.4	7.3	6.9	6.9–7.4 (7.2 ± 0.2)	**ML**	7.2	7.8	7.2–7.8 (7.5 ± 0.4)
LAHL	14.4	14.0	14.4	14.5	14.4	12.5	12.5–14.5 (14.0 ± 0.8)	**LAHL**	14.1	15.0	14.1–15.0 (14.6 ± 0.6)
PL	12.6	12.6	13.0	12.2	12.6	11.9	11.9–13.0 (12.5 ± 0.4)	**PL**	13.1	12.5	12.5–13.1 (12.8 ± 0.4)
TIB	14.2	13.3	13.3	13.3	13.4	12.4	12.4–14.2 (13.3 ± 0.6)	**TIB**	14.1	14.6	14.1–14.6 (14.3 ± 0.4)
HLL	45.1	44.5	44.5	45.1	44.9	39.61	39.6–45.1 (43.9 ± 2.1)	**HLL**	44.4	45.6	44.4–45.6 (45.0 ± 0.9)
HDL/ SVL	0.40	0.37	0.38	0.38	0.38	0.37	0.37–0.40 (0.38 ± 0.01)	**HDL/ SVL**	0.34	0.34	0.34–0.34 (0.34 ± 0.00)
HDW/ SVL	0.34	0.34	0.34	0.34	0.34	0.35	0.34–0.35 (0.34 ± 0.00)	**HDW/ SVL**	0.32	0.32	0.32–0.32 (0.32 ± 0.00)
HDW/ HDL	0.83	0.91	0.90	0.89	0.90	0.94	0.83–0.94 (0.90 ± 0.03)	**HDW/ HDL**	0.95	0.95	0.95–0.95 (0.95 ± 0.00)
SNT/ HDL	0.37	0.39	0.38	0.39	0.39	0.34	0.34–0.39 (0.38 ± 0.02)	**SNT/ HDL**	0.39	0.41	0.39–0.41 (0.40 ± 0.02)
IND/ HDW	0.30	0.28	0.29	0.28	0.28	0.31	0.28–0.31 (0.29 ± 0.01)	**IND/ HDW**	0.28	0.28	0.28–0.28 (0.28 ± 0.01)
IOD/ HDW	0.27	0.25	0.26	0.25	0.25	0.29	0.25–0.29 (0.26 ± 0.01)	**IOD/ HDW**	0.28	0.28	0.28–0.28 (0.28 ± 0.00)
EYE/ HDL	0.30	0.33	0.31	0.31	0.32	0.34	0.30–0.34 (0.32 ± 0.01)	**EYE/ HDL**	0.34	0.35	0.34–0.35 (0.34 ± 0.00)
TMP/ EYE	0.42	0.41	0.43	0.43	0.43	0.45	0.41–0.45 (0.43 ± 0.01)	**TMP/ EYE**	0.44	0.50	0.44–0.50 (0.47 ± 0.04)
ML/SVL	0.25	0.25	0.25	0.26	0.26	0.26	0.25–0.26 (0.26 ± 0.00)	**ML/ SVL**	0.24	0.25	0.24–0.25 (0.25 ± 0.01)
LAHL/ SVL	0.50	0.49	0.51	0.50	0.51	0.47	0.47–0.51 (0.50 ± 0.01)	**LAHL/ SVL**	0.47	0.49	0.47–0.49 (0.48 ± 0.01)
PL/SVL	0.43	0.44	0.46	0.42	0.44	0.45	0.42–0.46 (0.44 ± 0.01)	**PL/ SVL**	0.43	0.41	0.41–0.43 (0.42 ± 0.02)
TIB/SVL	0.49	0.47	0.47	0.46	0.47	0.47	0.46–0.49 (0.47 ± 0.01)	**TIB/ SVL**	0.47	0.47	0.47–0.47 (0.47 ± 0.01)
HLL/SVL	1.56	1.55	1.57	1.57	1.58	1.50	1.50–1.58 (1.55 ± 0.03)	**HLL/ SVL**	1.47	1.48	1.47–1.48 (1.48 ± 0.01)

Distribution and ecology. *Leptobrachella shimentaina* sp. nov. is known from its type locality Shimentai Nature Reserve, Yingde City, and the adjacent Luokeng Nature Reserve, Shaoguan City, Guangdong, China (Fig. 1; ca. 300–600 m a.s.l.). In the Hengshitang Protection Station of the Shimentai Nature Reserve, the new species is sympatric with *L. mangshanensis*. The new species inhabits primitive clear-water rocky streams surrounded by broad-leaved forest in karst landforms or granite landforms. From April to June, males were observed calling while perched on the rocks or under rocks in flowing streams, and females possessed mature oocytes.

Comparisons. In our phylogenetic analyses (Fig. 2, Table 3) *Leptobrachella shimentaina* **sp. nov.** clusters with *L. bashaensis*, *L. laui*, *L. liui*, *L. mangshanensis*, *L. maoershanensis*, and *L. yunkaiensis*, thus, these six species constitute the most important comparisons, for the purpose of diagnosis and recognition of the new species. In having wide fringes along lateral surfaces of toes in males, it can be distinguished from *L. bashaensis*, *L. mangshanensis* and *L. maoershanensis* (vs. lateral fringes narrow); by ventral coloration, grayish pink with distinct hazy brown speckling on chest and ventrolateral flanks; it can be distinguished from *L. bashaensis* (vs. creamy-white chest and belly with irregular black spots), *L. laui* (vs. creamy white with dark brown dusting on ventrolateral flanks), *L. liui* (vs. creamy white with dark brown spots on chest and ventrolateral flanks), *L. maoershanensis* (vs. creamy white chest and belly with irregular black spots), and *L. yunkaiensis* (vs. belly pink with distinct or indistinct speckling); by having dorsal skin with round granular tubercles and glandular folds, the new species can be further distinguished from *L. laui* (vs. dorsal skin lacking glandular folds), *L. mangshanensis* (vs. dorsal skin almost smooth with tiny transparent spines), and *L. yunkaiensis* (vs. dorsal skin shagreened with short skin ridges and raised warts); by dense small raised tubercles present on surface of chest and both sides of abdomen; it can be further distinguished from *L. mangshanensis*, *L. liui*, *L. yunkaiensis*, *L. maoershanensis* and *L. laui* (vs. ventral surface smooth); by having longitudinal ridges under toes

Figure 5. Morphological features of the paratypes of *Leptobrachella shimentaina* sp. nov.: **A1.** A female (SYS a004711 in situ; ventral view of the same specimen's hand [A2] and foot [A3]; **B.** Male SYS a007685 in situ; **C.** Male SYS a007686 in situ.

Table 3. Comparisons of selected diagnostic characters for the new species and its phylogenetically related congeners.

***Leptobrachella* spp.**	**Male SVL (mm)**	**Toes webbing**	**Fringes on toes**	**Longitudinal ridges under toes (interrupt + / not interrupt -)**	**Ventral coloration**	**Dorsal skin texture**
L. shimentaina **sp. nov.**	26.4–28.9	Rudimentary	Wide in males	-	Grayish pink with distinct hazy brown speckling on chest and ventrolateral flanks	Round granular tubercles with glandular folds
L. laui	24.8–26.7	Rudimentary	Wide	-	Creamy white with dark brown dusting on ventrolateral flanks	Round granular tubercles
L. liui	23.0–28.7	Rudimentary	Wide	+	Gray white to creamy white with dark brown spots on chest and ventrolateral flanks	Shagreened with numerous small tubercles, round warts and sparse short skin ridges
L. mangshanensis	22.2–27.8	Rudimentary	Narrow	-	Creamy white belly, scattered with white speckles	Almost smooth with tiny transparent spines, small tubercles and sparse short skin ridges
L. maoershanensis	25.2–30.4	Rudimentary	Narrow	-	Creamy white chest and belly with irregular black spots	With longitudinal folds
L. bashaensis	22.9–25.6	Rudimentary	Narrow	-	Creamy-white chest and belly with irregular black spots	Slightly shagreened with small tubercles
L. yunkaiensis	25.9–29.3	Rudimentary	Wide	-	Belly pink with distinct or indistinct speckles	Shagreened with short skin ridges and raised warts

continuous, with constrictions at interphalangeal articulations, it can be distinguished from *L. laui* (vs. longitudinal ridges without constrictions at interphalangeal articulations), *L. liui* (vs. longitudinal ridges interrupted at interphalangeal articulations), *L. maoershanensis* (vs. longitudinal ridges indistinct and not interrupted at interphalangeal articulations), and *L. yunkaiensis* (vs. longitudinal ridges without constrictions at interphalangeal articulations).

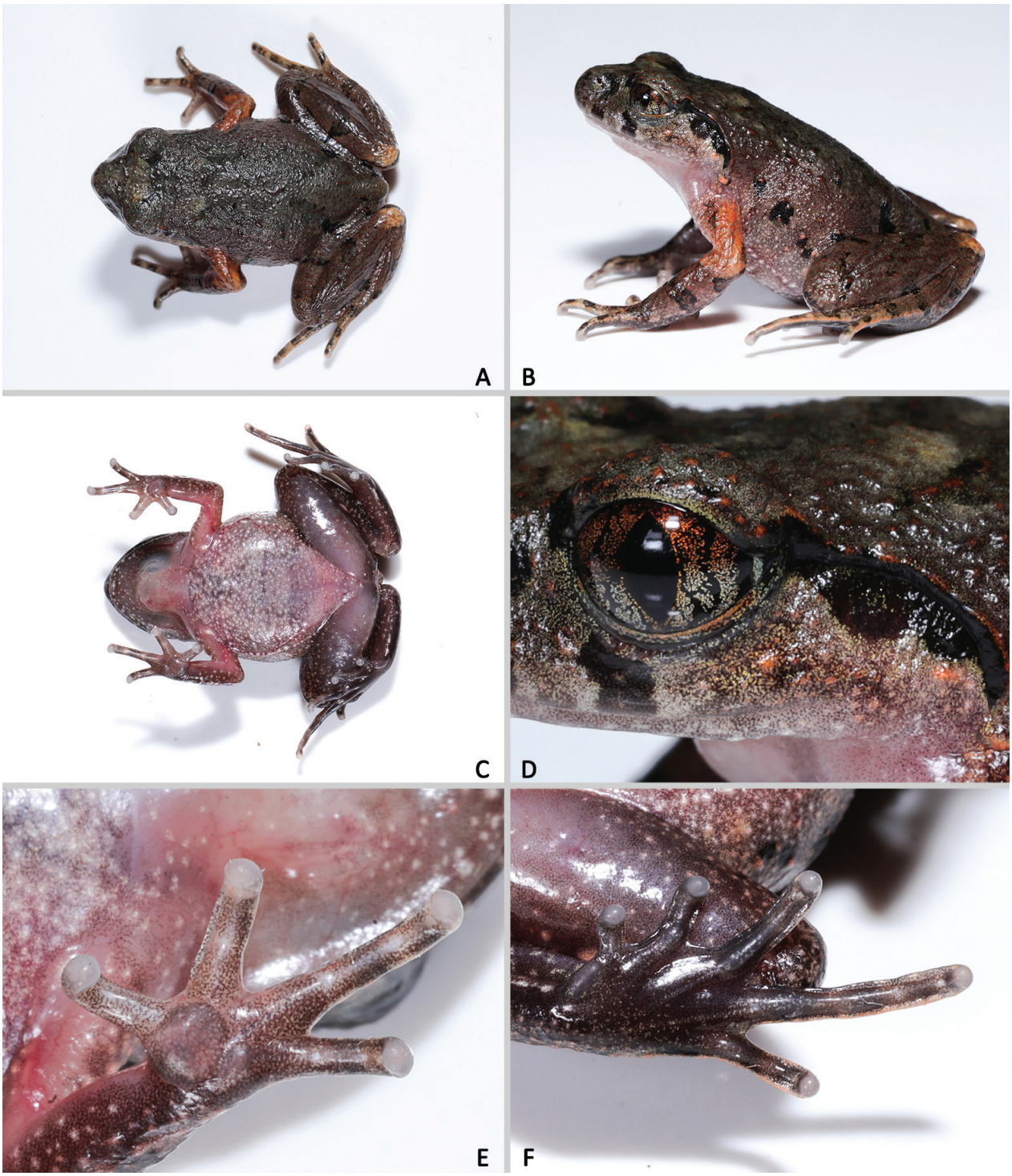

Figure 6. Morphological features of a paraype (SYS a007687) of *Leptobrachella shimentaina* sp. nov. in life.

Compared with the 26 known congeners of the genus *Leptobrachella* occurring south of the Isthmus of Kra, by the presence of supra-axillary and ventrolateral glands, *L. shimentaina* sp. nov. can easily be distinguished from *L. arayai*, *L. dringi*, *L. fritinniens*, *L. gracilis*, *L. hamidi*, *L. heteropus*, *L. kajangensis*, *L. kecil*, *L. marmorata*, *L. melanoleuca*, *L. maura*, *L. picta*, *L. platycephala*, *L. sabahmontana*, and *L. sola*, all of which lack supra-axillary and ventrolateral glands; and by its distinctly larger male body size, SVL 26.4–28.9 mm, *L. shimentaina* sp. nov. differs from the smaller *L. baluensis* (14.9–15.9), *L. brevicrus* (17.1–17.8), *L. bondangensis* (17.8), *L. fusca* (16.3), *L. itiokai* (15.2–16.7s), *L. juliandringi* (17.0–17.2), *L. mjobergi* (15.7–19.0), *L. natunae* (17.6), *L. parva* (15.0–16.9), and *L. palmata* (14.4–16.8); the female of *L. serasanae* (16.9), is also smaller than *L. shimentaina* sp. nov. (females 30.1–30.7).

For the remaining 60 members of the genus *Leptobrachella*, males *L. shimentaina* sp. nov. (SVL 26.4–28.9 mm) differs from males of the larger *L. chishuiensis* (30.8–33.4), *L. damingshanensis* (33.6–34.4), *L. eos* (33.1–34.7), *L. graminicola* (23.1–24.6), *L. neangi*

(30.9), *L. nahangensis* (40.8), *L. pyrrhops* (30.8–34.3), *L. sungi* (48.3–52.7), *L. tamdil* (32.3), and *L. zhangyapingi* (45.8–52.5); and from the smaller *L. aspera* (22.4), *L. applebyi* (19.6–22.3), *L. ardens* (21.3–24.7), *L. bidoupensis* (18.5–25.4), *L. feii* (21.5–22.8), *L. melica* (19.5–22.7), *L. murphyi* (23.2–24.9), *L. niveimontis* (22.5–23.6), *L. pluvialis* (21.3–22.3), and *L. rowleyae* (23.4–25.4). Through its possession of toes with rudimentary webbing and with wide lateral fringes in males, the new species can be distinguished from *L. bijie*, *L. dorsospina*, *L. flaviglandulosa*, *L. jinshaensis*, *L. purpuraventra*, *L. puhoatensis*, *L. shangsiensis*, *L. suiyangensis*, *L. tengchongensis*, *L. wuhuangmontis* and *L. yeae* (lateral fringes narrow), *L. bourreti*, *L. fuliginosa* (lateral fringes weak), *L. jinshaensis*, *L. kalonensis*, *L. maculosa*, *L. oshanensis*, *L. shiwandashan*, *L. tadungensis*, *L. ventripunctata* (no webbing or lateral fringes), *L. lateralis*, *L. namdongensis*, *L. macrops*, *L. minima*, *L. nyx* (no lateral fringes), and *L. pelodytoides* (extensive webbing and narrow lateral fringes), and additionally from *L. alpina*, *L. khasiorum*, *L. nokrekensis*, *L. yingjiangensis* (ventral coloration creamy white) and *L. purpurus* (ventral coloration dull white) by having greyish pink ventral coloration. By having black spots on flanks, it further differs from *L. aerea*, *L. botsfordi*, *L. crocea*, *L. firthi*, *L. isos*, *L. pallida*, *L. petrops*, and *L. tuberosa*, all of which lack black spots on the flanks.

Discussion

Studies of taxonomy and species diversity of the family Megophryidae have been challenged by morphological conservativeness among the majority of species in this clade (Rowley et al. 2015b; Wang et al. 2019). In recent years, the approach of integrative taxonomy has made substantial progress with this species-rich group, particularly with regards to our understanding of species boundaries in the genera *Leptobrachella* Smith, 1925 and *Boulenophrys* Fei, Ye & Jiang, 2016 (Lyu et al. 2021; Qi et al. 2021; AmphibiaWeb 2022; Frost 2022). Nonetheless, as more and more new species have been proposed, primarily based on molecular data (Chen et al. 2017, 2018; Mahony et al. 2017; Liu et al. 2018), detailed analyses of morphological characteristics, bioacoustics data, ecological information or other natural history data must also be provided to independently substantiate these claims (Lyu et al. 2020b, 2021). It is important that researchers remain vigilantly conservative and avoid taxonomic inflation within this species-rich family, particularly in light of geographically sparse, inadequate, poorly sampled surveys and increasingly atomized taxonomic partitioning in the absence of new data.

Leptobrachella bijie was described based on a single population from Bijie, northwestern Guizhou (Wang et al. 2019). Li et al. (2020) subsequently proposed *L. chishuiensis* from Chishui, northwestern Guizhou, and most recently, Wang et al. (2021) reported *L. bijie* from Huagaoxi Nature Reserve, southeastern Sichuan (Fig. 1). In our analysis, we found *Leptobrachella* populations from these three neighboring localities to cluster together with only very minor divergences and with strong support for their monophyly (BPP = 1.00 and BS = 100; Fig. 2). Diagnostic morphological character differences are quite subtle between *L. bijie* and *L. chishuiensis*(Li et al. 2020), and slight apparent "differences" may amount from human measurement error, such as snout-vent length of males (29.0–30.4 mm in *L. bijie* vs. SVL 30.8–33.4 in *L. chishuiensis*) and the internasal versus interorbital distances (IND = IOD in *L. bijie* vs. IND > IOD in *L. chishuiensis*). The specimen SYS a004955 (sample ID 41 in our Figs 1, 2) from Chishui is clustered with the type specimens of *L. chishuiensis* (without appreciable genetic divergence), however, its morphological characters inversely match those of *L. bijie*. For instance, its heels are just meeting when thighs are positioned at right angles to the body (vs. heels overlapping in *L. chishuiensis*), the tibia-tarsal articulation reaches forward to the middle of the eye (vs. tympanum to eye in *L. chishuiensis*). Li et al. (2020) performed bioacoustic analysis to support proposed taxonomic validity of *L. chishuiensis*, however, this study confused note and call intervals (comparing note interval in *L. chishuiensis* to call interval of *L. bijie*), which resulted in one apparently erroneous stated diagnostic "difference" (a shorter call interval in *L. chishuiensis*). The other difference (2 notes for *L. bijie* vs. 1–4 notes for *L. chishuiensis*) has been suggested to be only differences between populations rather than between species (Weaver et al. 2020). Geographically, the newly discovered population of *L. bijie* from southeastern Sichuan is much closer to the type locality of *L. chishuiensis* and any distinct barriers in geography (which might promote divergence) are absent. Therefore, we suspect *L. chishuiensis* should most likely be considered conspecific (and be synonymized) with *L. bijie*.

We also noticed the close relationship between the congeners *Leptobrachella alpina* and *L. purpurus*, leading to the problem of the taxonomic validity of *L. purpurus*. The latter species was described by Yang et al. (2018) based on two specimens, without comparison to the molecular data of *L. alpina*. However, whereas molecular data corresponding to *L. alpina* were provided (Chen et al. 2018), corresponding data for *L. purpurus* were not included. In our phylogenetic analysis, both "species" clustered together, with minimal "interspecific" divergences, and with inconsistent support for their monophyly (BPP = 0.99, BS = 83; Fig. 2). Accessible voucher material for these two species is limited (two males for *L. purpurus* and three males for *L. alpina*), and reported type localities of the two species are distant from each other with a distance over 340 km (Fig. 1). Therefore, we refrain from making taxonomic changes to *L. purpurus* until further studies, based on geopraphically comprehensive surveys, with robust, statistically-valid sample sizes, are conducted throughout southwestern Yunnan Province, to clarify or refute species' boundaries involving these two taxa.

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Appendix 1

Specimens examined:

Leptobrachella alpina **(n = 3):** China: Yunnan: Jingdong County: Mt. Wuliang: CIB 24353–24354; SYS a 003927.

Leptobrachella bijie **(n = 9):** China: Guizhou: Bijie City: SYS a007313–7320; China: Guizhou: Chishui City: SYS a004955.

Leptobrachella laui **(n = 26):** China: Hong Kong: SYS a002057 (Holotype), SYS a002058; China: Guangdong: Shenzhen City: SYSa 001505–1507, 1515–1521, 3471–3472, 5644–5645.

Leptobrachella liui **(n = 32):** China: Fujian: Mt. Wuyi: SYS a001572, 1596, 2478, 2479, 5925, 5926; China: Fujian: Mt. Daiyun: SYS a001736, 6010; China: Fujian: Mt. Longqi: SYS a002505, 2506; China: Guangdong: Mt. Tongguzhang: SYS a004733–4735; China: Guangdong: Mt. Fenghuang: SYS a003698–3699; China: Guangdong: Mt. Motianshi: SYS a007610–7613; China: Guangdong: Mt. Nankun: SYS a002020, 4497; China: Guangdong: Gutian Nature Reserve: SYS a002650; China: Jiangxi: Mt. Jiulian: SYS a002104–2105; China: Jiangxi: Mt. Tongbo: SYS a001702, 2059; China: Jiangxi: Mt. Yangjifeng: SYS a006667, 6672; China: Zhejiang: Jingning: SYS a002732–2735.

Leptobrachella mangshanensis **(n = 11):** China: Hunan: Mangshan Nature Reserve: SYS a008366; China: Guangdong: Nanling Nature Reserve: SYS a002828–2830, 5754; China: Guangdong: Shimentai Nature Reserve: SYS a005763, 6880; China: Guangdong: Mt. Tianjing: SYS a002806, 2809; China: Guangdong: Mt. Dadong: SYS a002847–2848.

Leptobrachella purpuraventra **(n = 15):** China: Guizhou: Bijie City: SYS a007277–7284, 7300–7306.

Leptobrachella yunkaiensis **(n = 8):** China: Guangdong: Maoming City: Dawuling Forestry Station: SYS a004664/CIB107272, SYS a004663, 4665–4669, 4690.

Supplementary material 1

Table S1

Authors: Jian Wang, Shuo Qi, Ke-Yuan Dai, Zhi-Tong Lyu, Zhao-Chi Zeng, Hong-Hui Chen, Yuan-Qiu Li, Yong-You Zhao, Yun-Ze Wang, Ying-Yong Wang

Data type: excel file

Explanation note: Collection localities, voucher data, and Genbank numbers (16S rRNA) for all *Leptobrachella* samples used in this study.

Link: https://doi.org/10.3897/zse.98.73162.suppl1

Supplementary material 2

Table S2

Authors: Jian Wang, Shuo Qi, Ke-Yuan Dai, Zhi-Tong Lyu, Zhao-Chi Zeng, Hong-Hui Chen, Yuan-Qiu Li, Yong-You Zhao, Yun-Ze Wang, Ying-Yong Wang

Data type: excel file

Explanation note: Uncorrected P-distance of 16S gene among 45 *Leptobrachella* species in this study.

Link: https://doi.org/10.3897/zse.98.73162.suppl2