Two new *Leptobrachella* species (Anura, Megophryidae) from the Yunnan-Guizhou Plateau, southwestern China

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**Abstract**

Two new toad species of the genus *Leptobrachella* are described from the Yunnan-Guizhou Plateau of China, based on the combination of molecular and morphological data. The description of *Leptobrachella aspera* Wang, Lyu, Qi & Wang, sp. nov. from Huanglianshan Nature Reserve represents the thirteenth *Leptobrachella* species known from Yunnan Province, and the description of *Leptobrachella dorsospina* Wang, Lyu, Qi & Wang, sp. nov. from Yushe Forest Park represents the sixth *Leptobrachella* species known from Guizhou Province. These new discoveries further emphasize the extremely high diversity of the *Leptobrachella* toads in these regions.

**Keywords**

*Leptobrachella aspera* sp. nov., *Leptobrachella dorsospina* sp. nov., molecular phylogeny, morphology, taxonomy
Introduction

The generic classifications within the family Megophryidae Bonaparte, 1850 have always been controversial. For example, recent comprehensive approaches have produced different taxonomic schemes for the genus *Megophrys* sensu lato Kuhl and Van Hasselt 1822 (Chen et al. 2017; Mahony et al. 2017; Liu et al. 2018; Li et al. 2020b). The taxonomy of another group of megophrid toads are facing the same problem: Chen et al. (2018) presented the first well-resolved phylogenetic hypothesis for the genera *Leptolalax* Dubois, 1983 and *Leptobrachella* Bonaparte, 1850. They tended towards the most conservative “one-genus option” pending the acquisition of additional data by assigning *Leptolalax* as a junior synonym of *Leptobrachella*. Their results also rejected the hypothesis that *Leptolalax* consists of two subgenera as proposed by Delorme et al. (2006) and Dubois et al. (2010). In this context, the genus *Leptobrachella* currently contains 82 species widely distributed from southern China, west to northeastern India, through Indochina to the island of Borneo (Frost 2020). *Leptobrachella* is a species-rich genus of megophrid frogs, and a large number of new species have been discovered in recent years due to the application of integrative taxonomy incorporating detailed morphological, bioacoustic and molecular analyses (Rowley et al. 2016, 2017; Yang et al. 2016; Yuan et al. 2017; Eto et al. 2018; Nguyen et al. 2018; Wang et al. 2019; Chen et al. 2020; Luo et al. 2020; Qian et al. 2020).

During recent field surveys in the Yunnan-Guizhou Plateau of southwestern China, a number of megophrid specimens were collected from Yushe Forest Park in western Guizhou (Fig. 1, site 1) and Huanglianshan Nature Reserve in southern Yunnan (Fig. 1, site 2), respectively. Morphologically, all the specimens can be assigned to the genus “*Leptolalax*” (now a junior subjective synonym of *Leptobrachella*), based on the following characters: (1) small or moderate size, snout-vent length not greater than 60.0 mm, (2) rounded finger tips, the presence of an elevated inner palmar tubercle not continuous to the thumb, (3) presence of macroglands on body including supra-axillary, pectoral, femoral and ventrolateral glands, (4) vomerine teeth absent, (5) tubercles on eyelids present, and (6) anterior tip of snout with whitish vertical bar (Dubois 1983; Matsui 1997, 2006; Lathrop et al. 1998; Delorme et al. 2006; Das et al. 2010). Although their generic allocation is without doubt, some characters of these specimens do not correspond to the diagnoses of any recognized species. Subsequent molecular analysis further revealed that these specimens represent two distinct evolutionary lineages. Considering both the morphological differences and molecular divergences, these specimens are described herein as two new species.

Materials and methods

Sampling

For the molecular analyses, a total of 80 sequences (nine muscle tissue samples was sequenced and 71 sequences obtained from GenBank) were used, including five sequences of the undescribed species from Guizhou, four sequences of the undescribed species
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from Yunnan, 69 sequences of 66 recognized congeners, and two out-group sequences of *Oreolalax rhodostigmatus* Hu & Fei, 1979 and *Leptobrachium tengchongensis* Yang & Huang, 2019, respectively (Table 1). Due to the presence of cryptic diversity within genus *Leptobrachella*, we chose sequences from type series or topotype specimens for molecular analysis if available to ensure the taxonomic identity of the species being studied.

**Figure 1.** Collection sites. Site 1-Yushe Forest Park, Shuicheng County, Guizhou Province, the type locality of *Leptobrachella dorsospina* sp. nov.; site 2-Huanglianshan Nature Reserve, Lyuchun County, Yunnan Province, the type locality of *L. aspera* sp. nov.; site 3-Xiaqiaogou Nature Reserve, Xichou County, Yunnan Province, the type locality of *L. feii*; and site 4-Daweishan Nature Reserve, Pingbian County, Yunnan Province, another distribution locality of *L. feii*.

**DNA Extraction, PCR, and sequencing**

DNA was extracted from muscle tissue using a DNA extraction kit from Tiangen Biotech (Beijing) Co., Ltd. The mitochondrial gene 16S ribosomal RNA gene (16S rRNA) fragment from each sample was sequenced. Fragments were amplified using the primer
pairs L3975 (5'-CGCCTGTTTACCAAAAACAT-3') and H4551 (5'-CCGGTCTGAACTCAGATCACGT-3') (Simon et al. 1994). PCR amplifications were performed in a 20 μl reaction volume with the following cycling conditions: an initial denaturing step at 95 °C for five min; 35 cycles of denaturing at 95 °C for 40 s, annealing at 53 °C for 40 s and extending at 72 °C for one min; and a final extending step of 72 °C for 10 min. PCR products were purified with spin columns. The purified products were sequenced with both forward and reverse primers using BigDye Terminator Cycle Sequencing Kit according to the guidelines of the manufacturer. The products were sequenced on an ABI Prism 3730 automated DNA sequencer in Shanghai Majorbio Biopharm Technology Co., Ltd. All sequences have been deposited in GenBank (Table 1).

**Phylogenetic analyses**

Sequences were aligned in Clustal X 2.0 (Thompson et al. 1997) with default parameters. For GenBank sequences which lack information for part of the missing segments, we filled the blank sites with “N”. The aligned data was trimmed allowing no gap positions and default parameters in Gblocks version 0.91b (Castresana 2000). We ran Jmodeltest v2.1.2 (Darriba et al. 2012) with Akaike and Bayesian information criteria on the alignment and obtained the best-fitting nucleotide substitution model of GTR + I + G. Phylogenetic analysis was using Bayesian inference (BI) in MrBayes 3.2.4 (Ronquist et al. 2012). 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 samples were discarded as burn-in. 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/). Genetic distances among all *Leptobrachella* samples were calculated in MEGA 6 using the uncorrected *p*-distance model, with pairwise deletion of gaps and missing data.

**Table 1.** Collection localities, voucher data and GenBank numbers (16S rRNA) for all samples used in this study.

| ID | Ingroup sp. nov. | Collection Locality | Voucher No. | GenBank No. |
|----|------------------|---------------------|-------------|-------------|
| 1  | *Leptobrachella* aspera | Huanglianshan Nature Reserve, Yunnan, China | SYS a007743 | MW046199 |
| 2  | *Leptobrachella* aspera | Huanglianshan Nature Reserve, Yunnan, China | SYS a007744 | MW046200 |
| 3  | *Leptobrachella* aspera | Huanglianshan Nature Reserve, Yunnan, China | SYS a007745 | MW046201 |
| 4  | *Leptobrachella* aspera | Huanglianshan Nature Reserve, Yunnan, China | SYS a007746 | MW046202 |
| 5  | *Leptobrachella* dorsospina | Yushu Forest Park, Shuicheng, Guizhou, China | SYS a004961 | MW046194 |
| 6  | *Leptobrachella* dorsospina | Yushu Forest Park, Shuicheng, Guizhou, China | SYS a004962 | MW046195 |
| 7  | *Leptobrachella* dorsospina | Yushu Forest Park, Shuicheng, Guizhou, China | SYS a004973 | MW046196 |
| 8  | *Leptobrachella* dorsospina | Yushu Forest Park, Shuicheng, Guizhou, China | SYS a004974 | MW046197 |
| 9  | *Leptobrachella* dorsospina | Yushu Forest Park, Shuicheng, Guizhou, China | SYS a004975 | MW046198 |
| 10 | *Leptobrachella feii* | Xiaojiaogou Nature Reserve, Yunnan, China | KIZ032625 | MT302635 |
| 11 | *Leptobrachella feii* | Xiaojiaogou Nature Reserve, Yunnan, China | KIZ048894 | MT302634 |
| 12 | *Leptobrachella feii* | Xiaojiaogou Nature Reserve, Yunnan, China | KIZ048972 | MT302636 |
| 13 | *Leptobrachella feii* | Xiaojiaogou Nature Reserve, Yunnan, China | KIZ048973 | MT302637 |
| 14 | *Leptobrachella* aerea | U Bo, Quang Binh, Vietnam | ZFMK 86362 | JN848409 |
| 15 | *Leptobrachella* alpina | Huangcaoling, Jingdong, Yunnan, China | KIZ046816 | MH055866 |
| 16 | *Leptobrachella* appleyei | Ngoc Linh, Kon Tum, Vietnam | AMS R 173778 | KR018108 |
| 17 | *Leptobrachella* arayai | Mesilau, Sabah, Malaysia | BORNEENSIS 22931 | AB847558 |
| 18 | *Leptobrachella* ardens | Kon Ka Kinh, Gia Lai, Vietnam | AMS R 176463 | KR018110 |
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| ID | Ingroup | Collection Locality | Voucher No. | GenBank No. |
|----|---------|---------------------|-------------|-------------|
| 19 | *Leptobrachella* kidoakensis | Hon Giao, Lam Dong, Vietnam | NCSCM 77321 | HU902883 |
| 20 | *Leptobrachella* bijie | Zhaozishan Nature Reserve, Guizhou, China | SYS a007320 | MK414539 |
| 21 | *Leptobrachella* botsfordii | Fansipan, Lao Cai, Vietnam | AMS R 176540 | MH055953 |
| 22 | *Leptobrachella* bourreti | Lao Cai, Vietnam | AMS R 177673 | KR018124 |
| 23 | *Leptobrachella* chnihuiensis | Chishui, Guizhou Province, China | CIBCS20190518047 | MT117053 |
| 24 | *Leptobrachella* crocea | Kon Tum, Vietnam | AMS R 173740 | MH055954 |
| 25 | *Leptobrachella* dringi | Gunung Mulu National Park, Sarawak, Malaysia | NMBE1056532 | KJ851298 |
| 26 | *Leptobrachella* es | Long Nai, Phongsaly, Laos | MNHN.2004.0274 | JN844852 |
| 27 | *Leptobrachella* fahlgandulina | Ngoc Linh Nature Reserve, Kon Tum, Vietnam | AMS R 176524 | JQ739206 |
| 28 | *Leptobrachella* fritinniens | Xiaoqiaogou Nature Reserve, Yunnan, China | KIZ032626 | MTJ06353 |
| 29 | *Leptobrachella* frisieniens | Base Camp of Mulu NP, Sarawak, Malaysia | KUHE 53571 | AB847557 |
| 30 | *Leptobrachella* fuliginosa | Phetchaburi, Thailand | KUHE 20174 | LC201987 |
| 31 | *Leptobrachella* gracilis | Camp 1 of Gunung Mulu NP, Sarawak, Malaysia | NMBE1056364 | KJ851300 |
| 32 | *Leptobrachella* hamidi | Bukit Lanjak, Malaysia | KEU 17545 | AB969286 |
| 33 | *Leptobrachella* heteropus | Larat, Malaysia | KEU 15486 | LC202005 |
| 34 | *Leptobrachella* ioe | Gia Lai, Vietnam | AMS R 176480 | KT824769 |
| 35 | *Leptobrachella* kjiangensis | Tioman, Malaysia | LSUC 4431 | LC202001 |
| 36 | *Leptobrachella* kalonensis | Song Luy, Bien Thuan, Vietnam | AMNH 191762 | KR018115 |
| 37 | *Leptobrachella* kajangensis | Cameron, Malaysia | KUHE 52440 | LC202004 |
| 38 | *Leptobrachella* khasiorum | Meghalaya, India | SDBDU 2009.329 | KY022303 |
| 39 | *Leptobrachella* laui | Tai Mo Shan, Hongkong, China | SYS a002057 | KM014546 |
| 40 | *Leptobrachella* liui | Guadun, Mt. Wuyi, Fujian, China | SYS a002479 | MH065574 |
| 41 | *Leptobrachella* macrosp | Phu Yen, Vietnam | PYU DTD-508 | MG787991 |
| 42 | *Leptobrachella* maculosa | Phuoc Binh, Ninh Thuan, Vietnam | ZFMM 96600 | KR018120 |
| 43 | *Leptobrachella* mangshanensis | Mangshan Nature Reserve, Hunan, China | MSZT201701 | MG1G2196 |
| 44 | *Leptobrachella* marixiensis | Maershan Nature Reserve, Guangxi, China | KIZ019385 | KY966030 |
| 45 | *Leptobrachella* marmonata | Annah Rais, Pahawang, Malaysia | KUHE 53192 | AB969287 |
| 46 | *Leptobrachella* maxima | Kinabalu, Malaysia | SP 21450 | AB874559 |
| 47 | *Leptobrachella* melanolouca | Sar Thani, Thailand | KUHE 19719 | LC201990 |
| 48 | *Leptobrachella* melica | Girachey, Ratana Khiri, Cambodia | MVZ 258197 | HM135599 |
| 49 | *Leptobrachella* minima | Chiangdao, Thailand | KEU 23733 | LC201980 |
| 50 | *Leptobrachella* nangagensis | Na Hang Nature Reserve, Tuyen Quang, Vietnam | ROM 7035 | MH055853 |
| 51 | *Leptobrachella* namdorogensis | Thanh Ha, Vietnam | VNUF A 2017.95 | MK655390 |
| 52 | *Leptobrachella* nivicornensis | Daxushan Nature Reserve, Yunnan, China | KIZ015734 | MT302618 |
| 53 | *Leptobrachella* nyc | Malipo, Yunnan, China | ROM 35606 | MH055814 |
| 54 | *Leptobrachella* obernensenis | Mr. Emei, Sichuan, China | SYS a001830 | KM014810 |
| 55 | *Leptobrachella* pallicida | Gia Rich, Lam Dong, Vietnam | UNS00510 | KR018112 |
| 56 | *Leptobrachella* pelodysnides | Tam Don, Vinh Phu, Vietnam | MVZ 223642 | AY326798 |
| 57 | *Leptobrachella* petrops | Tuyen Quang, Vietnam | VNMN 2016.0.6 | KY459998 |
| 58 | *Leptobrachella* picta | Gunung Kinabalu National Park, Sabah, Malaysia | UNIMAS 8705 | KJ851329 |
| 59 | *Leptobrachella* pluvisialis | Sa Pa, Lao Cai, Vietnam | MNHN: 1999.5675 | N844831 |
| 60 | *Leptobrachella* puhoaensis | Nghe An, Vietnam | AMS R184852 | KY849588 |
| 61 | *Leptobrachella* purpurea | Yingjiang, Yunnan, China | SYS a006531 | MG520555 |
| 62 | *Leptobrachella* purpuraventra | Wujiang Nature Reserve, Guizhou, China | SYS a007277 | MK414518 |
| 63 | *Leptobrachella* pyrrhos | Loc Bac, Lam Dong, Vietnam | ZMMU ABV-00176 | PK017576 |
| 64 | *Leptobrachella* quadrius | Son Tra, Da Nang, Vietnam | ITBCZ 4113 | MG682549 |
| 65 | *Leptobrachella* sakhabontana | Mahua, Crocker, Malaysia | BOREENSI 12454 | AB847550 |
| 66 | *Leptobrachella* shangsiensis | Shiwan, Guangxi, China | NHMG1401032 | MK094560 |
| 67 | *Leptobrachella* sola | Terengganu, Malaysia | KUHE 53244 | LC202011 |
| 68 | *Leptobrachella* suiyangensis | Suiyang, Guizhou, China | GZNU20180606002 | MK829648 |
| 69 | *Leptobrachella* suyi | Bac Giang, Vietnam | ZMMU-NAP-02269 | MH055859 |
| 70 | *Leptobrachella* taduogensis | Dak Nong, Vietnam | UNS00517 | KR018122 |
| 71 | *Leptobrachella* tengchongensis | Tengchong, Yunnan, China | SYS a004598 | KU892092 |
| 72 | *Leptobrachella* tuberosa | Kon Ka Kin National Park, Gia Lai, Vietnam | ZMMU-NAP-02275 | MH055959 |
| 73 | *Leptobrachella* ventripunctata | Xishuangbanna, Yunnan, China | SYS a001768 | KM014811 |
| 74 | *Leptobrachella* wubahuangmu | Mr. Wubahuang, Pabei, Guangxi, China | SYS a003485 | MH065577 |
| 75 | *Leptobrachella* wulinogens | Tianzishan Nature Reserve, Hunan, China | CSUFT 200 | MT303017 |
| 76 | *Leptobrachella* yingjiagensis | Yingjiang, Yunnan, China | SYS a006533 | MG520550 |
| 77 | *Leptobrachella* yunkaiensis | Yunkai Nature Reserve, Guangdong, China | SYS a004663 | MH055858 |
| 78 | *Leptobrachella* zhejiangensis | Chiang Mai, Thailand | KIZ07258 | MH055864 |
| 79 | *Leptobrachium* tengchongense | Tengchong, Yunnan, China | SYS a004603 | KX066876 |
| 80 | Orelalax rhodostigmatus | Da Fang, Guizhou, China | CIBZYCA746 | EF397248 |
Morphometrics

Measurements followed Fei et al. (2009) and Rowley et al. (2013), and were taken with a digital caliper to the nearest 0.1 mm. These measurements were as follows:

- **SVL**: snout-vent length (from tip of snout to vent);
- **HDL**: head length (from tip of snout to rear of jaws);
- **HDW**: head width (head width at commissure of jaws);
- **SNT**: snout length (from tip of snout to anterior corner of eye);
- **EYE**: eye diameter (diameter of exposed portion of eyeball);
- **IOD**: interorbital distance (minimum distance between upper eyelids);
- **IND**: internasal distance (distance between nares);
- **TMP**: tympanum diameter (horizontal diameter of tympanum);
- **TEY**: tympanum-eye distance (distance from anterior edge of tympanum to posterior corner of eye);
- **TIB**: tibia length (distance from knee to heel);
- **ML**: manus length (distance from tip of third digit to proximal edge of inner palmar tubercle);
- **PL**: pes length (distance from tip of fourth toe to proximal edge of the inner metatarsal tubercle);
- **LAHL**: length of lower arm and hand (distance from tip of the third finger to elbow);
- **HLL**: hindlimb length (distance from tip of fourth toe to vent).

Sex was determined by the presence of internal vocal sac openings, and the presence of eggs in abdomen seen via external inspection.

All specimens were fixed in 10% buffered formalin and later transferred to 70% ethanol for preservation, and deposited at the Museum of Biology, Sun Yat-sen University (SYS) and Chengdu Institute of Biology, the Chinese Academy of Sciences (CIB), China; tissue samples were preserved in 95% ethanol for molecular studies.

Comparative morphological data of *Leptobrachella* species were obtained from examination of museum specimens (see Appendix 1) and from the references listed in Table 2. Due to the high likelihood of undiagnosed diversity within the genus (Rowley et al. 2016; Yang et al. 2016), where available, we rely on examination of topotypic material and/or original species descriptions.

**Results**

The BI analyses are shown in Fig. 2 with Bayesian posterior probabilities (BPP) for major nodes > 0.90. Genetic distances among all *Leptobrachella* samples are given in the Suppl. material 1: Table S1. Comparative morphological data of all recognized *Leptobrachella* species occurring north of the Kra Isthmus are listed in Table 3.
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### Table 2. Data sources of the 82 currently known species of the genus *Leptobrachella*.

| ID | *Leptobrachella* species | Literature |
|----|--------------------------|------------|
| 1  | *L. aerea* (Rowley, Stuart, Richards, Phimmachak & Sivongsay, 2010) | Rowley et al. 2010c |
| 2  | *L. alpina* (Fei, Ye & Li, 1990) | Fei et al. 2009, 2016 |
| 3  | *L. applebyi* (Rowley & Cao, 2009) | Rowley and Cao 2009 |
| 4  | *L. arapai* (Matsui, 1997) | Matsui 1997 |
| 5  | *L. ardeni* (Rowley, Tran, Le, Dau, Peloso, Nguyen, Hoang, Nguyen & Ziegler, 2016) | Rowley et al. 2016 |
| 6  | *L. baliensis* Smith, 1931 | Dring 1983; Eto et al. 2015 |
| 7  | *L. bitje* Wang, Li, Li, Chen & Wang, 2019 | Wang et al. 2019 |
| 8  | *L. bidoupensis* (Rowley, Le, Tran & Hoang, 2011) | Rowley et al. 2011 |
| 9  | *L. bondangensis* Eto, Matsui, Hamidy, Munir & Iskandar, 2018 | Eto et al. 2018 |
| 10 | *L. botafordi* (Rowley, Dau & Nguyen, 2013) | Rowley et al. 2013 |
| 11 | *L. bourreti* (Dubois, 1983) | Ohler et al. 2011 |
| 12 | *L. brevicrus* Dring, 1983 | Dring 1983; Eto et al. 2015 |
| 13 | *L. crocea* (Rowley, Hoang, Le, Dau & Cao, 2010) | Rowley et al. 2010a |
| 14 | *L. damnena* Li, Liu, Wei & Wang, 2020 | Li et al. 2020a |
| 15 | *L. dringii* (Dubois, 1987) | Inger et al. 1995; Matsui and Dehling 2012 |
| 16 | *L. eau* (Ohler, Wollenberg, Grosjean, Hendrix, Vences, Ziegler & Dubois, 2011) | Ohler et al. 2011 |
| 17 | *L. feii* Chen, Yuan & Che, 2020 | Chen et al. 2020 |
| 18 | *L. firthi* (Rowley, Hoang, Dau & Cao, 2012) | Rowley et al. 2012 |
| 19 | *L. fritinniens* (Dehling & Matsui, 2013) | Dehling and Matsui 2013 |
| 20 | *L. fuliginosa* (Matsui, 2006) | Matsui 2006 |
| 21 | *L. flaviglandulosa* Chen, Wang & Che, 2020 | Chen et al. 2020 |
| 22 | *L. fusca* Eto, Matsui, Hamidy, Munir & Iskandar, 2018 | Eto et al. 2018 |
| 23 | *L. gracilis* (Günther, 1872) | Günther 1872; Dehling 2012b |
| 24 | *L. hamidi* (Matsui, 1997) | Matsui 1997 |
| 25 | *L. heteropus* (Boulenger, 1900) | Boulenger 1900 |
| 26 | *L. isos* (Rowley, Stuart, Neang, Hoang, Dau, Nguyen & Emmett, 2015) | Rowley et al. 2015a |
| 27 | *L. itiokai* Eto, Matsui & Nishikawa, 2016 | Eto et al. 2016 |
| 28 | *L. juliandringi* Eto, Matsui & Nishikawa, 2015 | Eto et al. 2015 |
| 29 | *L. kalonensis* (Rowley, Tran, Le, Dau, Peloso, Nguyen, Hoang, Nguyen & Ziegler, 2016) | Rowley et al. 2016 |
| 30 | *L. kecil* (Matsui, Belabut, Ahmad & Yong, 2009) | Matsui et al. 2009 |
| 31 | *L. keitai* (Dubois, 1983) | Das et al. 2010 |
| 32 | *L. lateralis* (Anderson, 1871) | Anderson 1871; Humtsoe et al. 2008 |
| 33 | *L. laui* (Sung, Yang & Wang, 2014) | Sung et al. 2014 |
| 34 | *L. liui* (Fei & Ye, 1990) | Fei et al. 2009; Sung et al. 2014 |
| 35 | *L. macrops* (Duong, Do, Ngo, Nguyen & Poyarkov, 2018) | Duong et al. 2018 |
| 36 | *L. maculosa* (Rowley, Tran, Le, Dau, Peloso, Nguyen, Hoang, Nguyen & Ziegler, 2016) | Rowley et al. 2016 |
| 37 | *L. mangshanensis* (Hou, Zhang, Hu, Li, Shi, Chen, Mo & Wang, 2018) | Hou et al. 2018 |
| 38 | *L. marandoniensis* (Yuan, Sun, Chen, Rowley & Che, 2017) | Yuan et al. 2017 |
| 39 | *L. marstonii* (Matsui, Zainudin & Nishikawa, 2014) | Matsui et al. 2014b |
| 40 | *L. maura* Inger, Lakim, Biun & Yambun, 1997 | Inger et al. 1997 |
| 41 | *L. melanoleuca* (Matsui, 2006) | Matsui 2006 |
| 42 | *L. melico* (Rowley, Stuart, Neang & Emmett, 2010) | Rowley et al. 2010b |
| 43 | *L. minima* (Taylor, 1962) | Taylor 1962; Ohler et al. 2011 |
| 44 | *L. mjobergi* Smith, 1925 | Eto et al. 2015 |
| 45 | *L. nanxangensis* (Lathrop, Murphy, Orlov & Ho, 1998) | Lathrop et al. 1998 |
| 46 | *L. natunae* (Günther, 1895) | Günther 1895 |
| 47 | *L. namdongensis* Hoang, Nguyen, Luu, Nguyen & Jiang, 2019 | Hoang et al. 2019 |
| 48 | *L. neangi* Stuart & Rowley, 2020 | Stuart and Rowley 2020 |
| 49 | *L. nivemontii* Chen, Poyarkov, Yuan & Che, 2020 | Chen et al. 2020 |
| 50 | *L. nokrekensis* (Mathew & Sen, 2010) | Mathew and Sen 2010 |
| 51 | *L. nys* (Ohler, Wollenberg, Grosjean, Hendrix, Vences, Ziegler & Dubois, 2011) | Ohler et al. 2011 |
| 52 | *L. oshanensis* (Liu, 1950) | Fei et al. 2009, 2016 |
| 53 | *L. pallida* (Rowley, Tran, Le, Dau, Peloso, Nguyen, Hoang, Nguyen & Ziegler, 2016) | Rowley et al. 2016 |
| 54 | *L. palmata* Inger & Stuebing, 1992 | Inger and Stuebing 1992 |
| 55 | *L. parva* Dring, 1983 | Dring 1983 |
| 56 | *L. pelodytoides* (Boulenger, 1893) | Boulenger 1893; Ohler et al. 2011 |
As shown by the phylogenetic result, *Leptobrachella* samples from Huanglianshan Nature Reserve are clustered in a distinct and robust monophyletic lineage with strong support (BPP 1.00). This lineage forms the sister taxon to *L. feii* occurring in Xiaoqiaogou Nature Reserve (BPP 1.00). The genetic distances between these two lineages are 3.0–3.4%, which is significantly larger than that among other recognized species (e.g., *p*-distance 2.6% between *L. liui* and *L. mangshanensis*). Detailed morphological examination also reveals a combination of characters that distinguish the specimens of the unnamed lineage from *L. feii* and other known congeners (see taxonomic comparison below). Therefore, based on the molecular and morphological differences, the population from Huanglianshan Nature Reserve is proposed as a new species, *Leptobrachella aspera* sp. nov.

Samples of the other unnamed lineage from Yushe Forest Park, cluster in another distinct and robust monophyletic lineage with strong support (BPP 1.00). This lineage is close to several species occurring in southwestern China, but its specific placement remains unresolved due to the insufficient support values. The smallest genetic distance between this lineage and another congener is 3.5% (vs. *L. purpuraventra*), which is significantly larger than that between other recognized species (e.g., *p*-distance 2.6% between *L. liui* and *L. mangshanensis*). Detailed morphological examination also reveals a combination of characteristics distinguishing the specimens of this lineage from all known congeners (see taxonomic comparison below). Therefore, based on the molecular and morphological differences, the population from Yushe Forest Park is proposed as a new species, *Leptobrachella dorsospina* sp. nov.

| ID | *Leptobrachella* species | Literature |
|----|--------------------------|------------|
| 58 | *L. petrops* (Rowley, Dau, Hoang, Le, Curaj & Nguyen, 2017) | Rowley et al. 2017a |
| 59 | *L. picta* (Malkmus, 1992) | Malkmus 1992 |
| 60 | *L. platycephala* (Dhelling, 2012) | Dhelling 2012a |
| 61 | *L. plusialis* (Ohler, Marquis, Swan & Grosjean, 2000) | Ohler et al. 2000, 2011 |
| 62 | *L. puhatenensis* (Rowley, Dau & Cao, 2017) | Rowley et al. 2017b |
| 63 | *L. purpura* (Yang, Zeng & Wang, 2018) | Yang et al. 2018 |
| 64 | *L. purpuraventra* (Wang, Li, Chen & Wang, 2019) | Wang et al. 2019 |
| 65 | *L. pyrrhops* (Poyarkov, Rowley, Gogoleva, Vassiljeva, Galoyan & Orlov, 2015) | Poyarkov et al. 2015 |
| 66 | *L. rowleyae* (Nguyen, Poyarkov, Le, Vo, Ninh, Duong, Murphy & Sang, 2018) | Nguyen et al. 2018 |
| 67 | *L. sabahmontana* (Matsui, Nishikawa & Yambun, 2014) | Matsui et al. 2014a |
| 68 | *L. serasanae* (Dring, 1983) | Dring 1983 |
| 69 | *L. shangienensis* (Chen, Liao, Zhou & Mo, 2019) | Chen et al. 2019 |
| 70 | *L. sola* (Matsui, 2006) | Matsui 2006 |
| 71 | *L. suijiangensis* (Luo, Xiao, Gao & Zhou, 2020) | Luo et al. 2020 |
| 72 | *L. suagi* (Lathrop, Murphy, Orlov & Ho, 1998) | Lathrop et al. 1998 |
| 73 | *L. tardungensis* (Rowley, Tran, Le, Dau, Peloso, Nguyen, Hoang & Ziegler, 2016) | Rowley et al. 2016 |
| 74 | *L. tamdil* (Sengupta, Sailo, Lalremmsanga, Das & Das, 2010) | Sengupta et al. 2010 |
| 75 | *L. tengchongensis* (Yang, Wang, Chen & Rao, 2016) | Yang et al. 2016 |
| 76 | *L. tuberosa* (Inger, Orlov & Darevsky, 1999) | Inger et al. 1999 |
| 77 | *L. ventripunctata* (Fei, Ye & Li, 1990) | Fei et al. 2009, 2016 |
| 78 | *L. wuhananmensis* (Wang, Yang & Wang, 2018) | Wang et al. 2018 |
| 79 | *L. wulingensis* (Qian, Xia, Cao, Xiao & Yang, 2020) | Qian et al. in publication |
| 80 | *L. yingjiangensis* (Yang, Zeng & Wang, 2018) | Yang et al. 2018 |
| 81 | *L. yunkaiensis* (Wang, Li, Lyu & Wang, 2018) | Wang et al. 2018 |
| 82 | *L. zhangyapingi* (Jiang, Yan, Suwannapoom, Chomdej & Che, 2013) | Jiang et al. 2013 |
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**Figure 2.** Bayesian Inference tree. The Bayesian posterior probabilities (BPP) > 0.90 were retained.
### Table 3. Comparisons of selected diagnostic characters for the new species described herein and congeners occurring north of the Kra Isthmus (modified from Rowley et al. 2017; Wang et al. 2019; Chen et al. 2020).

| Leptobrachella species | Male SVL (mm) | Black spots on flanks | Toe webbing | Toe fringes | Ventral coloration | Dorsal skin texture |
|------------------------|---------------|-----------------------|-------------|-------------|--------------------|---------------------|
| *L. aspera* sp. nov.   | 22.4          | Present               | Rudimentary | Narrow      | Creamy white with distinct dark patches on chest and abdomen | Rough with dense conical granules, tubercles, and glandular folds |
| *L. doraspinosa* sp. nov. | 28.7–30.5     | Present               | Rudimentary | Narrow      | Greyish white with black spots and orange pigmentation | Rough with dense conical granules, tubercles, glandular folds, and conical spines |
| *L. aerea*             | 25.1–28.9     | Absent                | Rudimentary | Wide        | Near immaculate creamy white, brown speckles on margins | Finely tuberculate |
| *L. alpina*            | 24.0–26.4     | Present               | Rudimentary | Wide in males | Creamy-white with dark spots | Relatively smooth, some with small warts |
| *L. applebyi*          | 19.6–22.3     | Present               | Rudimentary | Absent      | Reddish brown with white speckles | Smooth |
| *L. ardens*            | 21.3–24.7     | Present               | Absent      | Absent      | Reddish brown with white speckles | Smooth, finely shagreened |
| *L. bidoupensis*       | 18.5–25.4     | Present               | Rudimentary | Weak        | Reddish brown with white speckles | Smooth |
| *L. bijie*             | 29.0–30.4     | Present               | Rudimentary | Narrow      | White with distinct nebulous greyish speckles on chest and ventrolateral flanks | Shagreened and granular |
| *L. buttfordi*         | 29.1–32.6     | Absent                | Rudimentary | Narrow      | Reddish brown with white speckles | Shagreened |
| *L. bouretti*          | 28.0–36.2     | Present               | Rudimentary | Weak        | Creamy white | Relatively smooth, some with small warts |
| *L. crocea*            | 22.2–27.3     | Absent                | Rudimentary | Absent      | Bright orange | Highly tuberculate |
| *L. chishuiensis*      | 30.8–33.4     | Present               | Rudimentary | Narrow      | White with distinct nebulous greyish speckles on chest and ventrolateral flanks | Shagreened and granular |
| *L. cos*               | 33.1–34.7     | Absent                | Rudimentary | Wide        | Creamy white | Shagreened |
| *L. freii*             | 21.5–22.8     | Present               | Rudimentary | Narrow      | Creamy white with black blotches | Shagreened with small tubercles and ridge |
| *L. frithi*            | 26.4–29.2     | Absent                | Rudimentary | Wide in males | Creamy white | Shagreened with fine tubercles |
| *L. flaviglandulosa*   | 23.0–27.0     | Present               | Poorly developed | Narrow | Whitish with black speckles on margins | Shagreened with yellowish-brown tubercles |
| *L. fulgignosa*        | 28.2–30.0     | Present               | Rudimentary | Weak        | White with brown dusting | Nearly smooth with few tubercles |
| *L. insan*             | 23.7–27.9     | Absent                | Rudimentary | Wide in males | Creamy white with white dusting on margins | Mostly smooth, females more tuberculate |
| *L. kalonensis*        | 25.8–30.6     | Present               | Absent      | Absent      | Pale, speckled brown | Smooth |
| *L. khasiorum*         | 24.5–27.3     | Present               | Rudimentary | Wide        | Creamy white | Isolated, scattered tubercles |
| *L. laui*              | 24.8–26.7     | Present               | Rudimentary | Wide        | Creamy white with dark brown dusting on margins | Round granular tubercles |
| *L. lisa*              | 23.0–28.7     | Present               | Rudimentary | Wide        | Creamy white with dark brown spots on chest and margins | Round granular tubercles with glandular folds |
| *L. lateralis*         | 26.9–28.3     | Present               | Rudimentary | Absent      | Creamy white | Roughly granular |
| *L. macrosp*           | 28.0–29.3     | Present               | Rudimentary | Absent      | Greyish violet with white speckles | Roughly granular with larger tubercles |
| *L. maculata*          | 24.2–26.6     | Present               | Absent      | Absent      | Brown with few white speckles | Mostly smooth |
| *L. mangoebanensis*    | 22.2–27.8     | Present               | Rudimentary | Weak        | White speckles on throat and belly | Nearly smooth |
| *L. marcellinae*       | 25.2–30.4     | Present               | Rudimentary | Narrow      | Creamy white chest and belly with irregular black spots | With longitudinal folds |
| *L. melica*            | 19.5–22.7     | Present               | Rudimentary | Absent      | Reddish brown with white speckles | Smooth |
| *L. minima*            | 25.7–31.4     | Present               | Rudimentary | Absent      | Creamy white | Smooth |
| *L. naungangensis*     | 40.8          | Present               | Rudimentary | Absent      | Creamy white with light speckles on throat and chest | Smooth |
| *L. niveomontis*       | 22.5–23.6     | Present               | Rudimentary | Narrow      | Marbling with black speckles | Relatively smooth with small tubercules |
| *L. nobrekenensis*     | 26.0–33.0     | Present               | Rudimentary | Unknown     | Creamy white | Tubercles and longitudinal folds |
| *L. nyx*               | 26.7–32.6     | Present               | Rudimentary | Absent      | Creamy white with brown margins | Rounded tubercles |
| *L. namdongensis*      | 30.9          | Present               | Rudimentary | Absent      | Immaculate white, chest and belly with dark specking on outer margins | Low, round tubercles, more dense in posterior part of the back |
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| *Leptobrachella* species | Male SVL (mm) | Black spots on flanks | Toe webbing | Toe fringes | Ventral coloration | Dorsal skin texture |
|--------------------------|--------------|----------------------|-------------|-------------|------------------|-------------------|
| *L. neangi*              | -            | Present              | Weak (in females) | Absent (in females) | Light purplish gray with dark brown mottling on throat | Small, irregular bumps and ridges |
| *L. osmanensis*          | 26.6–30.7    | Present              | Absent       | Absent       | Whitish with no markings or only small, light grey spots | Smooth with few glandular ridges |
| *L. pallida*             | 24.5–27.7    | Absent               | Absent       | Absent       | reddish brown with white speckles | Tuberculate |
| *L. pelodogonida*        | 27.5–32.3    | Present, Wide        | Narrow       | Whith        | Whitish           | Small, smooth warts |
| *L. petrops*             | 23.6–27.6    | Absent               | Narrow       | Immaculate   | creamy white      | Highly tuberculate |
| *L. plusialis*           | 21.3–22.5    | Present, Rudimentary | Absent       | Dirty white with dark brown marbling | Smooth, Rattened tubercules on flanks |
| *L. pulcosterni*         | 24.2–28.1    | Present, Rudimentary | Narrow       | Whitish      | With longitudinal skin ridges | Shagreened with granules |
| *L. purpura*             | 25.0–27.5    | Present, Rudimentary | Wide         | Dull white with indistinct grey dusting | Smooth with numerous tiny tubercles |
| *L. purpuravana*         | 27.3–29.8    | Present, Rudimentary | Narrow       | Grey purple with distinct nebulous greyish speckles on chest and ventrolateral flanks | Shagreened with granules |
| *L. pyrhops*             | 30.8–34.3    | Present, Rudimentary | Absent       | Reddish brown with white speckles | Slightly shagreened |
| *L. rowleyae*            | 23.4–25.4    | Present              | Absent       | Pinkish milk-white to light brown chest and belly with numerous white speckles | Smooth with numerous tiny tubercles |
| *L. suijangensi*         | 28.7–29.7    | Present, Rudimentary | Narrow       | Yellowish creamy-white with marble texture chest and belly or with irregular light brown speckles | Shagreened with small granules |
| *L. sangi*               | 48.3–52.7    | Absent or small      | Wide         | White        | Granular |
| *L. tadangensi*          | 23.3–28.2    | Present              | Absent       | Reddish brown with white speckles | Smooth |
| *L. tamdi*               | 52.3         | Present              | Wide         | White        | Weakly tuberculate |
| *L. tengchongensi*       | 23.9–26.0    | Present, Rudimentary | Narrow       | White with dark brown blotches | Shagreened with small tubercles |
| *L. tuberosa*            | 24.4–29.5    | Absent               | Rudimentary  | Absent       | White with small grey spots/streaks | Highly tuberculate |
| *L. ventripunctata*      | 25.5–28.0    | Present, Rudimentary | Absent       | Chest and belly with dark brown spots | Longitudinal skin ridges |
| *L. wuhuangmontis*       | 25.6–30.0    | Present, Rudimentary | Narrow       | Greyish white mixed by tiny white and black dots | Rough, scattered with dense conical tubercles |
| *L. wulingensi*          | 22.7–30.5    | Present              | Rudimentary  | Narrow       | Translucent creamy white, with distinct or indistinct brown speckles at margins | Shagreened with sparse large warts, some with longitudinal ridges |
| *L. yingjiangensi*       | 25.7–27.6    | Present, Rudimentary | Wide         | Creamy white with dark brown flecks on chest and margins | Shagreened with small tubercles |
| *L. yunkaiensi*          | 25.9–29.3    | Present, Rudimentary | Wide         | Belly pink with distinct or indistinct speckles | Shagreened with short skin ridges and raised warts |
| *L. zhangyapingi*        | 45.8–52.5    | Absent               | Rudimentary  | Creamy-white with brown margins | Mostly smooth with distinct tubercles |

**Taxonomic accounts**

*Leptobrachella aspera* Wang, Lyu, Qi & Wang, sp. nov.
http://zoobank.org/4919B18E-B0D0-4329-90BF-8AC77280D263
Fig. 3

**Type material.** *Holotype.* SYS a007743, adult male, collected by Jian Wang, Yao Li and Yu-Long Li on 31 May 2019 from Huanglianshan Nature Reserve (22.89°N, 102.29°E; ca. 1930 m a.s.l.), Lyuchun County, Yunnan Province, China.

**Paratypes** (N = 3). Three adult females, SYS a007744–7745, SYS a007746/CIB116080, the same collection data as the holotype.

**Diagnosis.** (1) Small size (SVL 22.4 mm in a single adult male, 25.0–26.4 in three adult females), (2) dorsal skin rough, with dense conical granules, tubercles...
and glandular folds, (3) iris bicolored, amber on upper half and silver on lower half, (4) tympanum distinctly discernible, distinct black supratympanic line present, (5) absence of webbing and lateral fringes on fingers, toes with rudimentary webbing and narrow lateral fringes both in males and females, (6) longitudinal ridges under toes not interrupted at the articulations, (7) relative finger lengths I < IV < II < III, relative toe length I < II < V < III < IV, (8) heels just meeting, tibia-tarsal articulation reaches the region between middle of eye to anterior corner of eye, (9) dorsum greyish brown to yellowish brown grounding, with small light orange granules and distinct darker brown markings scattered with irregular light orange or greyish white pigmentation, (10) flanks with several enlarged dark patches with light yellowish green margin, (11) ventral surface creamy white, with distinct regular dark patches on chest and abdomen.

Figure 3. Morphological features in life. *Leptobrachella aspera* sp. nov., holotype SYS a007743.
Comparison. From the 26 known congeners of the genus *Leptobrachella* occurring south of the Kra Isthmus, the presence of supra-axillary and ventrolateral glands, can easily distinguish *L. aspera* sp. nov. 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 the supra-axillary and ventrolateral glands; and by the significantly larger body size, SVL 22.4 mm in a single male, *L. aspera* sp. nov. differs from the smaller *L. baluensis* (14.9–15.9 mm in males), *L. brevicrus* (17.1–17.8 mm in males), *L. bondangensis* (17.8 mm in male), *L. fusca* (16.3 mm in male), *L. itiokai* (15.2–16.7 mm in males), *L. juliandringi* (17.0–17.2 mm in males), *L. mjobergi* (15.7–19.0 mm in males), *L. natunae* (17.6 mm in one adult male), *L. parva* (15.0–16.9 mm in males), *L. palmata* (14.4–16.8 mm in males), and *L. serasanae* (16.9 mm in female).

*Leptobrachella aspera* sp. nov. is recovered as a sister taxon to *L. feii* in the phylogenetic tree (Fig. 2). However, the new species can be distinguished from *L. feii* by the following morphological characters: head relatively short, HDL/SVL 0.33–0.35 (vs. head relatively long, HDL/SVL 0.38–0.43); distinct regular dark patches on skin of chest and abdomen (vs. irregular black blotches scattered on skin of chest and belly); color of upper half of iris amber (vs. color of upper half of iris lighter, golden orange); ventrolateral glands forming an non-continuous line (vs. ventrolateral glands forming a continuous line); relative finger lengths I < IV < II < III (vs. relative finger lengths II < I < IV < III); tibio-tarsal articulation of adpressed limb reaching the region between middle of eye to anterior corner of eye (vs. tibio-tarsal articulation of adpressed limb reaching beyond eye).

While *Leptobrachella pluvialis* is distributed in the same mountain range on the Vietnamese side and possesses similar body size (Ohler et al. 2000), it can be separated from *L. aspera* sp. nov. by the following characters: (1) smooth dorsal skin with flattened tubercles on flanks (vs. rough dorsal skin with dense conical granules in *L. aspera* sp. nov.), (2) absence of webbing on toes (vs. rudimentary webbing on toes in *L. aspera* sp. nov.), and (3) relatively longer hindlimbs, the tibia-tarsal articulation reaching to the nostril (vs. relatively shorter hindlimbs, the tibia-tarsal articulation reaching the region between middle of eye to anterior corner of eye in *L. aspera* sp. nov.).

For the remaining 54 members of the genus *Leptobrachella*, in having SVL 22.4 mm in a single male, *L. aspera* sp. nov. differs from the larger *L. aerea* (25.1–28.9 in males), *L. alpina* (24.0–28.9 mm in males), *L. bijie* (29.0–30.4 mm in males), *L. botsfordi* (29.1–32.6 mm in males), *L. bourretni* (28.0–36.2 mm in males), *L. chishuiensis* (30.8–33.4 in males), *L. eos* (33.1–34.7 mm in males), *L. firthi* (26.4–29.2 mm in males), *L. flaviglandulosa* (23.0–27.0 mm in males), *L. fuliginosa* (28.2–30.0 mm in males), *L. isos* (23.7–27.9 mm in males), *L. kalonensis* (25.8–30.6 mm in males), *L. khasiorum* (24.5–27.3 mm in males), *L. laui* (24.8–26.7 mm in males), *L. lateralis* (26.9–28.3 mm in males), *L. macrops* (28.0–29.3 mm in males), *L. maculosa* (24.2–26.6 mm in males), *L. minima* (25.7–31.4 mm in males), *L. nahangensis* (40.8 mm in male), *L. nokrekensis* (26.0–33.0 mm in males), *L. nyx* (26.7–32.6 mm in males), *L. neangi* (30.9 mm in male), *L. namdongensis* (30.9 mm in male), *L. oshanensis* (26.6–30.7 mm in males), *L. pallida
Jian Wang et al. / ZooKeys 995: 97–125 (2020)

By presence of black spots on flanks, the new species can be distinguished from *L. crocea*, versus absence of black spots on flanks; by rudimentary webbing on toes, the new species can be distinguished from *L. ardens*, versus absence of webbing on toes; by narrow lateral fringes on toes, the new species can be distinguished from *L. applebyi*, *L. ardens*, *L. crocea*, and *L. melica*, all having no lateral fringes on toes, and from *L. liui*, having wide lateral fringes on toes; by the creamy white ventral coloration and distinct regular dark patches on the chest and abdomen, the new species can be distinguished from *L. applebyi*, *L. ardens*, *L. bidoupensis*, and *L. melica*, all having reddish brown ventral coloration with white specks, from *L. crocea*, having bright orange ventral coloration, from *L. mangshanensis*, lacking dark skin patches on the chest and abdomen, from *L. liui*, having creamy white ventral coloration with dark brown spots on the chest and margins, and from *L. niveimontis*, having marbling ventral coloration with black speckling; by rough dorsal skin with dense conical granules, tubercles and glandular folds, the new species can be distinguished from *L. applebyi*, *L. ardens*, *L. bidoupensis*, *L. mangshanensis*, *L. melica*, and *L. niveimontis*, all having smooth dorsal skin.

**Description of holotype.** Adult male. Body size small, SVL 22.4 mm. Head length slightly larger than head width, HDW/HDL 0.99; snout slightly protruding, projecting slightly beyond margin of the lower jaw; nostril closer to snout than eye; canthus rostralis gently rounded; loreal region slightly concave; interorbital space flat, internarial distance greater than interorbital distance, IND/IOD 1.07; pineal ocellus absent; pupil vertical; snout length longer than eye diameter, SNT/EYE 1.26; tympanum distinct, rounded, and slightly concave, diameter smaller than that of the eye and larger than tympanum-eye distance, TMP/EYE 0.52 and TEY/TMP 0.44; upper margin of tympanum in contact with supratympanic ridge; distinct black supratympanic line present; vomerine teeth absent; vocal sac openings slit-like, paired, located posterolaterally on floor of mouth in close proximity to the margins of the 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 < IV < II < III; nuptial pad absent; subarticular tubercles absent; large, rounded inner palmar tubercle distinctly separated from small, rounded outer palmar tubercle; webbing and lateral fringes on fingers absent. Tips of toes rounded, slightly swollen; relative toe length I < II < V < III < IV; subarticular tubercles absent; distinct longitudinal dermal ridges present under the 3rd to 5th toes, not interrupted; large, oval inner metatarsal tubercle
present, outer metatarsal tubercle absent; toes webbing rudimentary; narrow lateral fringes present on all toes. Tibia 47% of snout-vent length; tibiotarsal articulation reaching to anterior corner of eye; heels slightly overlapping when thighs are appressed at right angles with respect to body.

Dorsal skin rough, with dense conical granules, tubercles and glandular folds; ventral skin smooth; sparse tiny tubercles present on surface of chest; pectoral gland and femoral gland oval; the size of pectoral glands almost equal to tips of fingers and femoral glands; femoral gland situated on posterodorsal surface of thigh, closer to knee than to vent; supra-axillary glands raised. Ventrolateral glands distinctly visible, raised, forming an incomplete line.

**Coloration of holotype in life.** Dorsum greyish brown with small light orange granules, distinct darker brown markings scattered with irregular light orange and greyish white pigmentations. A dark brown inverted triangular pattern between the anterior corners of the eyes in connection with a dark brown W-shaped marking in the interorbital region, which is also connected to a W-shaped marking between the axillae. Tympanum dark brown. Small light orange granules present on dorsum of body and limbs; a dark brown blotch under the eye; transverse dark brown bars present on dorsal surface of limbs and digits; distinct dark brown patches with light yellowish green margin on flanks from groin to axilla; elbow and upper arms with distinct coppersy orange coloration.

Ventral surface of throat, chest, and belly creamy white; presence of distinct nebulous greyish speckles present on throat, and distinct dark patches on chest and abdomen; ventral surface of limbs greyish purple, scattered with greyish white spots and small patches. Supra-axillary gland coppersy orange; femoral, pectoral, and ventrolateral glands greyish white. Iris bicolored, amber on upper half and silver on lower half.

**Coloration of holotype in preservative (Fig. 4A).** Dorsum of body and limbs dark brown; transverse bars on limbs become more distinct; dark brown patterns, markings and spots on the back become indistinct, orange pigmentations become dark brown, greyish white pigmentations become dark grey. Ventral surface of limbs and surface of throat light brown, surface of abdomen greyish white, nebulous speckles on throat absent, dark patches on chest, abdomen and flanks become more distinct, light yellowish green margin of patches on flanks absent. Supra-axillary, femoral, pectoral, and ventrolateral glands greyish white.

**Variation.** Measurements and body proportions are listed in Table 4. Nonsexual characters of all the female paratypes (SYS a007744, 7745, 7746) match the overall characters of the holotype except that: the dorsum is greyish brown in the holotype SYS a007743 (vs. yellowish brown in the paratypes); the size of the pectoral glands are almost equal to the tips of the fingers and the femoral glands (vs. the size of the pectoral glands are larger than the tips of fingers and the femoral glands in the paratypes); the tibia-tarsal articulation reaches forward to the anterior corner of the eye in the holotype (vs. the tibia-tarsal articulation reaches forward to the middle of the eye in the paratypes SYS a007745, 7746); the ventral skin of the thighs smooth (vs. the ventral skin of the thighs rough with dense raised tubercles in the paratypes).
Figure 4. Morphological features in preserved specimens of **A** Leptobrachella aspera** sp. nov., holotype SYS a007743 **B** Leptobrachella dorsospina** sp. nov., holotype SYS a004974. Ellipse selected region showing the tiny spines on dorsal skin.
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Table 4. Measurements and body proportions of *Leptobrachella aspera* sp. nov.

| Voucher | SYS a 007743 | SYS a 007744 | SYS a 007745 | SYS a 007746 |
|---------|--------------|--------------|--------------|--------------|
| Sex     | Male         | Female       | Female       | Female       |
| SVL     | 22.4         | 25.3         | 25.0         | 26.4         |
| HDL     | 8.1          | 9.5          | 9.5          | 9.6          |
| HDW     | 8.0          | 9.3          | 9.2          | 9.0          |
| SNT     | 5.7          | 3.8          | 3.8          | 3.4          |
| IND     | 2.5          | 2.3          | 2.7          | 2.7          |
| IOD     | 2.3          | 2.5          | 2.5          | 2.5          |
| EYE     | 2.9          | 3.2          | 3.2          | 3.1          |
| TMP     | 1.5          | 1.8          | 1.9          | 1.6          |
| TEY     | 0.7          | 1.0          | 1.0          | 0.8          |
| ML      | 5.9          | 7.0          | 6.6          | 6.3          |
| LAHL    | 11.2         | 13.5         | 12.7         | 12.6         |
| PL      | 10.1         | 11.7         | 10.2         | 11.1         |
| TIB     | 10.6         | 12.4         | 11.9         | 11.9         |
| HLL     | 34.4         | 41.5         | 40.4         | 39.1         |
| HDL/SVL | 0.36         | 0.37         | 0.38         | 0.36         |
| HDW/SVL | 0.36         | 0.37         | 0.37         | 0.34         |
| HDW/HDL | 0.99         | 0.98         | 0.97         | 0.94         |
| SNT/HDL | 0.16         | 0.15         | 0.15         | 0.13         |
| IND/HDW | 0.31         | 0.25         | 0.29         | 0.30         |
| IOD/HDW | 0.29         | 0.27         | 0.27         | 0.28         |
| IND/IOD | 1.07         | 0.91         | 1.08         | 1.09         |
| EYE/HDL | 0.36         | 0.34         | 0.34         | 0.32         |
| TMP/EYE | 0.52         | 0.56         | 0.60         | 0.51         |
| ML/SVL  | 0.26         | 0.28         | 0.26         | 0.24         |
| LAHL/SVL| 0.50         | 0.53         | 0.51         | 0.48         |
| PL/SVL  | 0.45         | 0.46         | 0.41         | 0.42         |
| TIB/SVL | 0.47         | 0.49         | 0.48         | 0.45         |
| HLL/SVL | 1.53         | 1.64         | 1.61         | 1.48         |

**Etymology.** The specific epithet, *aspera*, is a Latin adjective which means rough, in reference to the dorsal skin texture of the new species. According to its type locality, we suggest its English common name as “Huanglianshan Leaf Litter Toad”, and the Chinese name “Huang Lian Shan Zhang Tu Chan (黄连山掌突蟾)”.

**Distribution and habits.** Currently, *Leptobrachella aspera* sp. nov. is known only from its type locality Huanglianshan Nature Reserve, near the border between China and Vietnam. The new species was found along a drainage ditch of a mountainous road. The road was surrounded by broad-leaved forest at an altitude ca. 1930 m and not close to any hillstreams. Males were not heard calling during the field survey from 31 May to 1 June 2019.

*Leptobrachella dorsospina* Wang, Lyu, Qi & Wang, sp. nov.
http://zoobank.org/B0EA8FA8-0193-43BF-AA93-6D010467CF84
Fig. 5

**Type material. Holotype.** SYS a004974, adult male, collected by Zhi-Tong Lyu and Run-Lin Li on 21 June 2016 from Yushe Forest Park (26.47°N, 104.80°E; ca. 2100 m a.s.l.), Shuicheng District, Liupanshui City, Guizhou Province, China.
Paratypes (N = 6). An adult male, SYS a004977, and five adult females, SYS a004961/CIB116081, SYS a 004962, SYS a004973, 4975, 4976, collected by Zhi-Tong Lyu and Run-Lin Li on 20–21 June 2016 from the same locality as the holotype.

Diagnosis. (1) Small size (SVL 28.7–30.5 mm in two adult males, 32.1–39.8 mm in five adult females), (2) dorsal skin rough, with dense conical granules, tubercles, glandular folds and conical spines, (3) iris bicolored, light orange on upper half and silver on lower half, (4) tympanum distinctly discernible, distinct black supratympanic line present, (5) absence of webbing and lateral fringes on fingers, toes with rudimentary webbing and narrow lateral fringes both in males and females, (6) longitudinal ridges under toes interrupted at the articulations, (7) relative finger lengths II = IV < I < III, relative toe length I < II < V < III < IV, (8) heels slightly overlapping, tibia-tarsal articulation reaches forward to the posterior corners of eyes, (9) dorsum greyish brown to dark brown grounding, with distinct darker brown markings and scattered with irregular light greyish brown pigmentations and yellowish brown spots, (10) flanks with several enlarged dark patches positioned longitudinally in two rows, (11) ventral surface greyish white with black spots and orange pigmentations.

Comparison. Compared with the 26 known congeners of the genus Leptobrachella occurring south of the Kra Isthmus, L. dorsospina sp. nov. can be easily distinguished by the presence of supra-axillary and ventrolateral glands, 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 are lacking the supra-axillary and ventrolateral glands; and by the significantly larger body size, SVL 28.7–30.5 mm in two adult male, L. dorsospina sp. nov. differs from the smaller L. baluensis (14.9–15.9 mm in males), L. brevicrus (17.1–17.8 mm in males), L. bondangensis (17.8 mm in male), L. fusca (16.3 mm in male), L. itiokai (15.2–16.7 mm in males), L. juliandringi (17.0–17.2 mm in males), L. mjobergi (15.7–19.0 mm in males), L. natuna (17.6 mm in one adult male), L. parva (15.0–16.9 mm in males), L. palmata (14.4–16.8 mm in males), and L. serasanae (16.9 mm in female).

Leptobrachella dorsospina sp. nov. can be easily distinguished from Leptobrachella aspera sp. nov. by having distinctly larger body size, SVL 28.7–30.5 mm in males, 32.1–39.8 mm in females (vs. SVL 22.4 mm in male, 25.0–26.4 in females); conical spines on dorsal skin present (vs. absent); black spots on flanks in one row (vs. black spots on flanks in two rows); ventral skin greyish white with black spots and orange pigmentations (vs. ventral skin creamy white with distinct dark patches on chest and abdomen); longitudinal ridges under toes interrupted at the articulations (longitudinal ridges under toes not interrupted at the articulations).

For the remaining 56 members of the genus Leptobrachella, in having SVL 28.7–30.5 mm in two males, L. dorsospina sp. nov. differs from the larger L. eos (33.1–34.7 mm in males), L. nahangensis (40.8 mm in male), L. sungi (48.3–52.7 mm in males), L. tamdil (32.3 mm in male), and L. zhangyapingi (45.8–52.5 mm in males); and from the smaller L. alpina (24.0–26.4 mm in males), L. applebyi (19.6–22.3 mm in males), L. ardens (21.3–24.7 mm in males), L. bidoupensis (18.5–25.4 mm in males), L. crocea (22.2–27.3 mm in males), L. feii (21.5–22.8 mm in males), L. flaviglandulosa (23.0–27.0 mm in males), L. isos (23.7–27.9 mm in males), L. khasiorum (24.5–
Two new *Leptobrachella* species from the Yunnan-Guizhou Plateau of China

27.3 mm in males), *L. laui* (24.8–26.7 mm in males), *L. maculosa* (24.2–26.6 mm in males), *L. mangshanensis* (22.2–27.8 mm in males), *L. melica* (19.5–22.7 mm in males), *L. niveimontis* (22.5–23.6 mm in males), *L. pallida* (24.5–27.7 mm in males), *L. petrops* (23.6–27.6 mm in males), *L. pluvialis* (21.3–22.3 mm in males), *L. puhoatensis* (24.2–28.1 mm in males), *L. purpura* (25.0–27.5 mm in males), *L. rowleyae* (23.4–25.4 mm in males), *L. tadungensis* (23.3–28.2 mm in males), *L. tengchongensis* (23.9–26.0 mm in males), *L. ventripunctata* (25.5–28.0 mm in males), and *L. yingjiangensis* (25.7–27.6 mm in males). By having black spots on the flanks, *L. dorsospina* sp. nov. can be distinguished from *L. aerea*, *L. botsfordi*, *L. firthi*, and *L. tuberosa*, all of which

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**Figure 5.** Morphological features in life. *Leptobrachella dorsospina* sp. nov., holotype SYS a004974.
lack black spots on the flanks. By having rough dorsal skin with conical spines, the new species can be distinguished from *L. bijie*, *L. chishuiensis*, *L. liui*, *L. maoershanensis*, *L. pyrrhops*, *L. purpuraventra*, *L. suiyangensis*, *L. wuhuangmontis*, *L. wulingensis*, and *L. yunkaiensis* (dorsal skin lacking spines); and from *L. bourreti*, *L. fuliginosa*, *L. kalonensis*, *L. minima*, *L. oshanensis*, and *L. pelodytoides* (dorsal skin smooth). By having narrow lateral fringes on the toes, the new species can be distinguished from *L. lateralis*, *L. macrops*, *L. nyx*, *L. pyrrhops*, *L. namdongensis* and *L. neangi*, all of which lack lateral fringes on the toes. The new species can be separated from the remaining *L. nokrekensis* by having greyish white ventral coloration with black patches and orange pigmentations (vs. creamy white), and having dense short glandular folds on the dorsal surface (vs. only a few glandular folds on the dorsal surface).

**Description of holotype.** Adult male. Body size rather small, SVL 30.5 mm. Head length slightly larger than head width, HDW/HDL 0.99; snout slightly protruding, projecting slightly beyond margin of the lower jaw; nostril closer to snout than eye; canthus rostralis gently rounded; loreal region slightly concave; interorbital space flat, internarial distance smaller than interorbital distance, IND/IOD 0.91; pineal ocellus absent; vertical pupil; snout length larger than eye diameter, SNT/EYE 1.29; tympanum distinct, rounded, and slightly concave, diameter smaller than that of the eye and larger than tympanum-eye distance, TMP/EYE 0.43 and TEY/TMP 0.50; upper margin of tympanum in contact with supratympanic ridge; distinct black supratympanic line present; vomerine teeth absent; vocal sac openings slit-like, paired, located posterolaterally on floor of mouth in close proximity to the margins of the 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 II = IV < I < III; nuptial pad absent; subarticular tubercles absent; large, rounded inner palmar tubercle distinctly separated from small, rounded outer palmar tubercle; absence of webbing and lateral fringes on fingers. Tips of toes rounded, slightly swollen; relative toe length I < II < V < III < IV; subarticular tubercles absent; distinct longitudinal dermal ridges present under the 3rd to 5th toes, interrupted; large, oval inner metatarsal tubercle present, outer metatarsal tubercle absent; toes webbing rudimentary; narrow lateral fringes present on all toes. Tibia 44% of snout-vent length; tibiotarsal articulation reaches to posterior corner of eye; heels slightly overlapping when thighs are appressed at right angles with respect to body.

Dorsal skin rough, with dense conical granules, tubercles, glandular folds and conical spines; ventral skin smooth; pectoral gland and femoral gland oval; the size of pectoral glands almost equal to tips of fingers and femoral glands; femoral gland situated on posteroventral surface of thigh, closer to knee than to vent; supra-axillary glands raised. Ventrolateral glands distinctly visible, raised, forming an incomplete line.

**Coloration of holotype in life.** Dorsum greyish brown with distinct darker brown markings on sides and scattered with irregular light greyish brown pigmentations and yellowish brown spots. An indistinct, darker brown inverted triangular pattern between anterior corners of the eyes, connected to an indistinct dark brown W-shaped marking between the axillae. Dense translucent spines present on dorsal skin of body
and limbs. Upper 2/3 of the tympanum dark brown, lower 1/3 light orange, scattered with tiny coppery orange spots. Small greyish white and light brown granules present on the dorsum of the body and limbs; a dark brown vertical bar under the eye; transverse dark brown bars on the dorsal surface of the limbs and digits; distinct dark brown patches on the flanks, from groin to axilla; elbow and upper arms with distinct light orange coloration.

Ventral surface of throat, chest, and belly greyish white; throat with light brown speckles, chest, and abdomen with distinct dark patches; ventral surface of limbs dark grey, scattered with greyish white spots and small patches. Supra-axillary gland light orange; femoral, pectoral, and ventrolateral glands greyish white. Iris bicolored, light orange on upper half and silver on lower half.

**Coloration of holotype in preservative (Fig. 4B).** Dorsum of body and limbs dark brown; transverse bars on limbs, dark brown patterns, markings, and spots on back become indistinct, light greyish brown pigmentation and yellowish spots absent. Translucent spines on dorsal skin of body and limbs become grey. Ventral surface of limbs and surface of throat light brown, surface of abdomen greyish white, dark patches on chest, abdomen and flanks become more distinct. Supra-axillary, femoral, pectoral, and ventrolateral glands greyish white.

**Variations.** Measurements and body proportions are listed in Table 5. All the female paratypes match the overall characters of the holotype except that: the dorsum

| Voucher | SYS a004977 | SYS a004974 | SYS a004961 | SYS a004962 | SYS a004973 | SYS a004975 | SYS a004976 |
|---------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|
| Sex     | Male        | Male        | Female      | Female      | Female      | Female      | Female      |
| SVL     | 28.7        | 30.5        | 36.1        | 57.3        | 39.8        | 32.1        | 33.8        |
| HDL     | 10.3        | 10.8        | 12.8        | 12.4        | 12.9        | 11.3        | 12.0        |
| HDW     | 10.6        | 10.7        | 11.9        | 12.9        | 13.2        | 11.8        | 12.2        |
| SNT     | 4.5         | 4.2         | 5.1         | 5.4         | 5.8         | 5.0         | 4.8         |
| IND     | 3.1         | 3.2         | 3.6         | 3.9         | 4.0         | 3.7         | 3.4         |
| IOD     | 3.4         | 2.9         | 3.5         | 3.4         | 3.3         | 3.0         | 2.9         |
| EYE     | 3.5         | 3.7         | 3.9         | 3.7         | 4.3         | 4.2         | 3.8         |
| TMP     | 1.7         | 1.6         | 2.3         | 2.3         | 2.6         | 2.1         | 2.1         |
| TEY     | 1.1         | 0.8         | 1.3         | 1.4         | 1.5         | 1.2         | 1.1         |
| ML      | 7.4         | 7.3         | 8.8         | 7.7         | 9.1         | 7.8         | 7.6         |
| LAHL    | 14.1        | 14.2        | 17.1        | 16.8        | 17.5        | 16.2        | 15.9        |
| PL      | 12.1        | 12.8        | 14.9        | 14.5        | 15.5        | 13.9        | 13.6        |
| TIB     | 13.5        | 13.4        | 15.5        | 16.3        | 16.6        | 14.9        | 14.5        |
| HLL     | 41.7        | 42.7        | 49.1        | 49.9        | 52.9        | 46.8        | 48.0        |
| HDL/SVL | 0.36        | 0.35        | 0.35        | 0.33        | 0.32        | 0.35        | 0.36        |
| HDW/SVL | 0.37        | 0.35        | 0.33        | 0.35        | 0.33        | 0.37        | 0.36        |
| HDW/HDL | 1.03        | 0.99        | 0.93        | 1.04        | 1.02        | 1.04        | 1.02        |
| SNT/HDL | 0.44        | 0.39        | 0.40        | 0.44        | 0.45        | 0.44        | 0.40        |
| IND/HDW | 0.29        | 0.30        | 0.30        | 0.30        | 0.30        | 0.31        | 0.28        |
| IOD/HDW | 0.32        | 0.27        | 0.29        | 0.26        | 0.25        | 0.25        | 0.24        |
| EYE/HDL | 0.34        | 0.34        | 0.30        | 0.30        | 0.33        | 0.37        | 0.32        |
| TMP/EYE | 0.49        | 0.43        | 0.59        | 0.62        | 0.60        | 0.50        | 0.55        |
| ML/SVL  | 0.26        | 0.24        | 0.24        | 0.21        | 0.23        | 0.24        | 0.22        |
| LAHL/SVL| 0.49        | 0.47        | 0.47        | 0.45        | 0.44        | 0.50        | 0.47        |
| PL/SVL  | 0.42        | 0.42        | 0.41        | 0.39        | 0.39        | 0.43        | 0.40        |
| TIB/SVL | 0.47        | 0.44        | 0.43        | 0.44        | 0.42        | 0.46        | 0.43        |
| HLL/SVL | 1.45        | 1.40        | 1.36        | 1.34        | 1.33        | 1.46        | 1.42        |
is greyish brown in the holotype SYS a004974 (vs. dark brown in the paratypes SYS a004961, 4962), and black spots on the ventral skin are more dense and distinct in the paratypes SYS a004961, 4962.

**Etymology.** The specific epithet, *dorsospina*, is in reference to the conical spines on the dorsal surface of body in the new species. According to its type locality, we suggest its English common name as “Shuicheng Leaf Litter Toad”, and the Chinese name “Shui Cheng Zhang Tu Chan (水城掌突蟾)”.

**Distribution and habits.** Currently, *Leptobrachella dorsospina* sp. nov. is known only from its type locality, Yushe Forest Park, which is near the border between Guizhou and Yunnan. The new species was found on the surface of fallen leaves by the clear-water rocky hill-stream in well-preserved montane evergreen broadleaf forest (ca. 2100 m a.s.l.). Males were not heard calling.

**Discussion**

In the phylogenetic tree, the *Leptobrachella pelodytoides* (voucher number: MVZ 223642) sample from Tam Dao, northern Vietnam is clustered together with the typotypic *L. ventripunctata* (voucher number: SYS a001768) sample from Xishuangbanna, Yunnan, China, with a genetic divergence of only 1.5% (Fig. 2, Suppl. material 1: Table S1), which is of a intraspecific level. In addition, the type locality of *L. pelodytoides* is Thao [= Thamo], Kayah State, Myanmar, which is geographically distant from northern Vietnam with a distance over 900 km. Considering the above, we recommend that the specimen MVZ 223642 be reappraised as *L. ventripunctata*.

Yunnan and Guizhou are both largely within the species-rich Dian freshwater zoogeographical dominion (Huang et al 2020). Spanning the Indo-Burma Hotspot and the Mountains of Southwest China Hotspot (Tordoff et al. 2012), Yunnan Province has for long been considered as one of the most biodiverse regions in China and its flora and fauna have attracted much attention. However, Guizhou Province, which also shares the Yunnan-Guizhou Plateau, remains relatively neglected; knowledge of biodiversity levels and patterns are seriously lacking. In recent years, large numbers of discoveries have been made from Guizhou, dramatically raising the number of frog species known from the region (Zhang et al. 2017; Li et al. 2018a, b, 2019a, b, 2020a; Lyu et al. 2019; Wang et al. 2019; Luo et al. 2020; Wei et al. 2020). Further comprehensive surveys are urgently needed to determine the true diversity of the amphibians of Guizhou Province.

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Appendix 1
Specimens examined

**Leptobrachella alpina** (n = 6): China: Yunnan Province: Jingdong County: Mt. Wuliang: CIB 24353 (holotype), CIB 24354; SYS a003927.

**Leptobrachella bijie** (n = 8): China: Guizhou: Bijie City: SYS a007313–7320.

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

**Leptobrachella liui** (n = 18): China: Fujian Province: Mt. Wuyi: CIB 24355 (holotype), CIB 24356, SYS a001571–1578, 1595–1599, 2478–2479, 5925–5826.

**Leptobrachella mangshanensis** (n = 5): China: Guangdong: Nanling Nature Reserve: SYS a002827–2830, 5754.

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

**Leptobrachella tengchongensis** (n = 6): China: Yunnan Province: Baoshan City: Mt. Gaoligong: SYS a004600 (holotype), 4596–4599, 4601–4602.

**Leptobrachella wuhuangmontis** (n = 12): China: Guangxi Province: Pubei County: Mt. Wuhuang: SYS a003500/CIB107274, SYS a000578, 0580–0581, 3485–3489, 3499, 3504–3506.

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

Supplementary material 1

Table S1. Pairwise distances based on 16S gene among all sample used in this study
Authors: Jian Wang, Zhi-Tong Lyu, Shuo Qi, Zhao-Chi Zeng, Wen-Xiang Zhang, Long-Shan Lu, Ying-Yong Wang
Data type: phylogenetic
Explanation note: Genetic distances among all *Leptobrachella* samples.
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