

## A new species of *Leptobrachella* Smith 1925 (Anura: Megophryidae) from Thanh Hoa Province, Vietnam

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**Abstract.** Based on the results of molecular and morphological systematics analyses, a new species, *Leptobrachella namdongensis*, is recognised from Nam Dong Conservation Area in Thanh Hoa Province, Vietnam. Genetic divergences in the 16S rRNA gene between the new form and other species in the genus range from 4.7 to 21.0% and average at approximately 24%. The new species is most similar to *L. petrops* and *L. puhoatensis*, but can be distinguished from them and other congeners by a combination of the following morphological characters: size medium (30.9 mm in the adult male and 32.1–35.3 mm in adult females); head wider than long; tympanum distinct; throat immaculate white, chest and belly with dark specking on outer margins; toes with basal webbing; supratympanic fold edged by a distinct black line; inter-orbital region with distinct black blotches; iris bicoloured, upper half copper, fading to golden in its lower half; head without dorsolateral markings.

**Key words.** Nam Dong Conservation Area, phylogenetics, Vietnam, taxonomy

### INTRODUCTION

The genus *Leptobrachella* was originally described by Smith (1925) with the type species *Leptobrachella mjobergi* Smith from Sarawak (Malaysia). Dubois (1980) erected a new genus *Leptolalax* with the type species *Leptobrachium gracile* Günther. However, based on the results of Chen et al. (2018), Frost (2019) synonymised *Leptolalax* with *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), but left problems that require resolving in the future. The genus *Leptobrachella* currently contains 74 species with a wide distribution throughout northeastern India, southern China, and Southeast Asia (Frost, 2019). Most species in the genus “*Leptolalax*” have a high morphological similarity,

and morphological characters alone are often not sufficient to distinguish species (Rowley et al., 2016), with the exception of *Leptobrachella (sensu stricta)*. Delineating species boundaries with acoustics and molecular systematic analyses has helped scientists discover more new species of *Leptobrachella*. In Vietnam, 19 new species from this genus have been described since 2010.

During our recent surveys in Thanh Hoa Province, Vietnam, specimens of a medium-sized species of Megophryidae were collected from Nam Dong Conservation Area. Morphological examination revealed the species is a representative of *Leptobrachella* based on the following characters: (1) the presence of an elevated inner metacarpal tubercle not continuous on to the thumb; (2) the presence of macro glands on body (including supra-axillary, pectoral, femoral, ventrolateral glands, and chest glands); (3) the absence of vomerine teeth; and (4) the anterior tip of snout with whitish vertical bar (Dubois, 1980, 1983; Lathrop et al., 1998; Matsui, 1997, 2006; Delorme et al., 2006; Fei et al., 2009, 2012; Nguyen et al., 2018). However, the species is distinct from other known species in the genus by suite morphological differences and genetic divergences. Therefore, we describe this population as a new species of *Leptobrachella* herein.

### MATERIAL AND METHODS

**Sampling.** Three field surveys were conducted in Nam Dong Conservation Area, Quan Hoa District, Thanh Hoa Province, Vietnam (Fig. 1) in May and July 2017 and April 2018 by V.Q. Luu, N.V. Ha, O.V. Lo, T.V. Pham (hereafter Luu et al.). Geographic coordinates and elevation were obtained using a Garmin GPSMAP 62sc. After photography, specimens were euthanised in a closed vessel with a piece

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Fig. 1. Map showing the type locality (red circle) of *Leptobrachella namdongensis*, new species in Thanh Hoa Province, northern Vietnam (Nam Dong Conservation Area). Red square is the location of Pu Hu NR. Yellow triangle is the type locality of *Leptobrachella petrops*, black triangle is a known distribution point of *Leptobrachella petrops*, yellow rhombus is the type locality of *Leptobrachella puhoatensis*.

of cotton wool containing ethyl acetate (Simmons, 2002), fixed in 80% ethanol for five hours, and then later transferred to 70% ethanol for permanent storage. Tissue samples were preserved separately in 95–100% ethanol prior to fixation. Sex was determined by the direct observation of calling males in the field or by gonadal dissection. In total, seven specimens were obtained (Table 4); IEBR 4512 and IEBR 4513 are deposited in the collections of the Institute of Ecology and Biological Resources (IEBR), VNMN 2019.04 and VNMN 2019.05 at the Vietnam National Museum of Nature (VNMN), and VNUF A.2017.37, VNUF A.2017.95 and VNUF A.2018.15 at the Vietnam National University of Forestry (VNUF), Hanoi, Vietnam.

**Molecular systematics analysis.** In this study, four samples of the new population were amplified for ~540 base pairs fragment of the 16S rRNA mitochondrial gene (Table 1). This gene was selected as it has been used in many other recent studies on the genus *Leptobrachella* (Rowley et al., 2016; 2017b; 2017a). Tissue samples were extracted using TIANamp Genomic DNA kit (TIANGEN BIOTECH, Beijing, China), following the manufacturers' instructions. Total DNA was amplified using PCR Eppendorf. PCR volume was 25  $\mu$ l, which included 12  $\mu$ l of Mastermix, 6  $\mu$ l of water, 1  $\mu$ l of each primer at concentration of 10 pmol/ $\mu$ l, and 5  $\mu$ l of DNA. Primers used in PCR and sequencing were as follows: LR-N-13398 (5'-CGCCTGTTTACCAAAAACAT-3'; forward) and LR-J 12887 (5'-CCGGTCTGAACTCAGATCACGT-3';

reverse) (Simon et al., 1994). PCR conditions: 94°C for 5 minutes for initial denaturation; 35 cycles of denaturation at 94°C for 30 s, annealing at 56°C for 30 s, and extension at 72°C for 45 s; and the final extension at 72°C for 7 minutes. PCR products were sent to Tsingke Biological Technology company for sequencing (<http://www.tsingke.net>). The new sequences are deposited in GenBank under the accession numbers MK965389-MK965392 (Table 1).

In addition to the four newly collected samples, we used 59 available sequences of 16S rRNA for 59 species from GenBank (Rowley et al., 2017b; 2017a; Chen et al., 2018) for phylogenetic analyses of the genus *Leptobrachella*. All the selected species are morphologically similar to the newly discovered population. Sequences of *Leptobrachium* cf. *chapaense* and *Megophrys major* were included in the analysis as outgroup (Rowley et al., 2017a). Locality information and accession numbers for all sequences included in the analysis are listed in Table 1.

Phylogenetic trees were constructed by using maximum likelihood (ML) and Bayesian inference (BI). Chromas Pro software (Technelysium Pty Ltd., Tewantin, Australia) was used to edit the sequences, which were aligned using the ClustalW (Thompson et al., 1997) option in MEGA 7.0 (Kumar et al., 2016) with default parameters and subsequently optimised manually in BioEdit 7.0.5.2 (Hall, 1999). We then checked the initial alignments by eye and adjusted slightly.

Table 1. GenBank accession numbers, and associated samples that were used in this study. All sequences generated by this study have accession numbers MK965389-MK965392.

	Species	Voucher no	GenBank no.	Locality
1	<i>L. aerea</i>	RH60165	JN848437	Vietnam, Quang Binh Province
2	<i>L. alpina</i>	KIZ046816	MH055866	China, Yunnan, Caiyanghe
3	<i>L. applebyi</i>	AMS R171703	HM133597	Vietnam, Quang Binh Province
4	<i>L. arayai</i>	BORNEENSIS 22931	AB847558	Malaysia, Borneo
5	<i>L. ardens</i>	VNMN 04707	KR018109	Vietnam, Gia Lai Province
6	<i>L. bidoupensis</i>	AMS R173134	HQ902880	Vietnam, Lam Dong Province
7	<i>L. bijie</i>	SYS a007313/CIB 110002	MK414532	China, Guizhou, Zhaozishan, Bijie City, Nature Reserve
8	<i>L. botsfordi</i>	AMSR176540	MH055952	Vietnam, Mt. Fansipan
9	<i>L. bourreti</i>	AMS R177673	KR018124	Vietnam, Lao Cai Province
10	<i>L. crocea</i>	SYS:a007313	MH055956	Vietnam, Quang Nam
11	<i>L. dringi</i>	KUHE:55610	AB847553	Malaysia, Borneo
12	<i>L. eos</i>	MNHN:2004.0278	JN848450	Laos, Phongsaly Province
13	<i>L. firthi</i>	AMS R176524	JQ739206	Vietnam, Kon Tum Province
14	<i>L. fritinniens</i>	KUHE 55371	AB847557	Malaysia, Borneo
15	<i>L. gracilis</i>	KUHE 55624	AB847560	Malaysia, Borneo
16	<i>L. hamidi</i>	KUHE 17545	AB969286	Malaysia, Borneo
17	<i>L. heteropa</i>	KUHE 15487	AB530453	Malaysia, Peninsula
18	<i>L. isos</i>	VNMN A 2015.4	KT824769	Vietnam, Gia Lai Province
19	<i>L. kajangensis</i>	LSUHC:4439	LC202002	Malaysia
20	<i>L. kalonensis</i>	IEBR A.2014.15	KR018114	Vietnam, Binh Thuan Province
21	<i>L. kecil</i>	KUHE:52440	LC202004	Malaysia
22	<i>L. khasiorum</i>	SDBDU 2009.329	KY022303	India, East Khasi Hills, Meghalaya
23	<i>L. laui</i>	SYS A002057	KM014546	China, Shenzhen
24	<i>L. liui</i>	SYS A001620	KM014549	China, Jiangxi Province
25	<i>L. macrops</i>	ZMMU-A5823	MG787993	Vietnam, Phu Yen Prov., Hon Den Mt.
26	<i>L. maculosa</i>	ZFMK 96600	KR018120	Vietnam, Ninh Thuan Province
27	<i>L. mangshanensis</i>	MSZTC201703	MG132198	China, Hunan
28	<i>L. maoershanensis</i>	SYSa002898	MH055930	China, Guangxi, Mao'er Shan
29	<i>L. marmorata</i>	ZFMK 96600	AB969289	Vietnam, Ninh Thuan Province
30	<i>L. maura</i>	SP 21450	AB847559	Malaysia, Borneo
31	<i>L. melanoleuca</i>	KIZ024598	MH055970	Thailand
32	<i>L. melica</i>	MVZ 258198	HM133599	Cambodia, Ratanakiri Province
33	<i>L. minima</i>		JN848369	Thailand, Chiangmai Province
34	<i>L. nahangensis</i>	ZMMU-NAP-02259	MH055854	Vietnam, Tuyen Quang, Na Hang Nature Reserve
35	<i>L. namdongensis</i> new species	VNUF A.2017.37, VNUF A.2017.95, VNMN2019.04, IEBR 4512	MK965389– MK965392	Vietnam, Thanh Hoa Province

Species	Voucher no	GenBank no.	Locality
36 <i>L. nyx</i>	AMNH A163810	DQ283381	Vietnam, Ha Giang Province
37 <i>L. oshanensis</i>	SYS A001830	KM014810	China, Sichuan Province
38 <i>L. pallida</i>	UNS00510	KR018112	Vietnam, Lam Dong Province
39 <i>L. petrops</i>	VNMN 2016 A.06	KY459999	Vietnam, Tuyen Quang Province
40 <i>L. picta</i>	UNIMAS 8705	KJ831295	Malaysia, Borneo
41 <i>L. pluvialis</i>	MNHN:1999.5675	JN848391	Vietnam, Lao Cai Province
42 <i>L. puhoatensis</i>	AMSR184852	KY849588	Vietnam, Nghe An Province
43 <i>L. purpuraventra</i>	SYS:a007306	MK414531	China: Guizhou, Bijie City, Zhaozishan Nature Reserve,
44 <i>L. purpura</i>	KFY515	MG520355	China, Yunnan Province, Yingjiang
45 <i>L. pyrrhops</i>	ZMMU A-5208	KP017578	Vietnam, Lam Dong Province
46 <i>L. sabahmontana</i>	BORNEENSIS 12632	AB847551	Malaysia, Borneo
47 <i>L. shangsiensis</i>	NHMG<CHN>:1401032	MK095460	China, southern Guangxi
48 <i>L. sola</i>	KU_RMB20973	MH055973	Malaysia
49 <i>L. sungi</i>	ZMMU-NAP-06580	MH055863	Vietnam, Phu Tho, Xuan Son National Park
50 <i>L. tadungensis</i>	UNS00515	KR018121	Vietnam, Dak Nong Province
51 <i>L. tengchongensis</i>	SYSa003766	MH055897	China, Yunnan
52 <i>L. tuberosa</i>	ZMMU-NAP-02275	MH055959	Vietnam, Gia Lai, Kon Ka Kinh National Park
53 <i>L. ventripunctata</i>	MNHN 2005.0116	LC201978	Laos, Phongsaly Province
54 <i>L. wuhuangmontis</i>	SYSa003485	MH605577	China, Guangxi, Pubei County, Mt. Wuhuang,
55 <i>L. yingjiangensis</i>	SYS a006537	MG520359	China, Yunnan Province, Yingjiang
56 <i>L. yunkaiensis</i>	SYS a004663	MH605584	China, Guangdong, Maoming City, Dawuling Forest Station,
57 <i>L. zhangyapingi</i>	KIZ07258	JX069979	Thailand, Chiangmai Province
58 <i>L. baluensis</i>	BORN:8595	LC056794	Malaysia, Borneo
59 <i>L. itiokai</i>	KUHE:55898	LC137806	Malaysia, Sarawak
60 <i>L. parva</i>	KUHE:55308	LC056791	Malaysia, Borneo
61 <i>Leptobrachium</i> cf. <i>chapaense</i>	AMS R171623	KR018126	Vietnam, Lao Cai Province
62 <i>Megophrys major</i>	AMS R173870	KY476333	Vietnam, Kon Tum Province

Prior to ML and BI phylogenetic analyses, we chose the optimum substitution models for entire sequences using Kakusan 4 (Tanabe, 2011) based on the Akaike information criterion (AIC). The BI was performed in MrBayes 3.2 (Ronquist et al., 2012). The BI summarised two independent runs of four Markov Chains for 10,000,000 generations. A tree was sampled every 100 generations and a consensus topology was calculated for 70,000 trees after discarding the first 30,001 trees (burn-in = 3,000,000) (Nguyen et al., 2017). We checked parameter estimations and convergence using Tracer version 1.5 (Rambaut & Drummond, 2009). The strength of nodal support in the ML tree was analysed using non-parametric bootstrapping (MLBS) with 1,000 replicates. We regarded tree nodes in the ML tree with bootstrap values

of 75% or greater as sufficiently resolved (Hillis & Bull, 1993; Huelsenbeck & Hillis, 1993), and nodes with a BPP of 95% or greater as significant in the BI analysis (Leaché & Reeder, 2002).

**Morphological systematics analyses.** Comparative morphological data were obtained from literature for descriptions for 41 species of *Leptobrachella* found in Indochina and surrounding parts of Southeast Asia. All comparative morphological data are presented in Table 2.

The following measurements were taken from the seven fixed specimens of the new population (Table 4) using a digital caliper to the nearest 0.1 mm, based off Rowley et

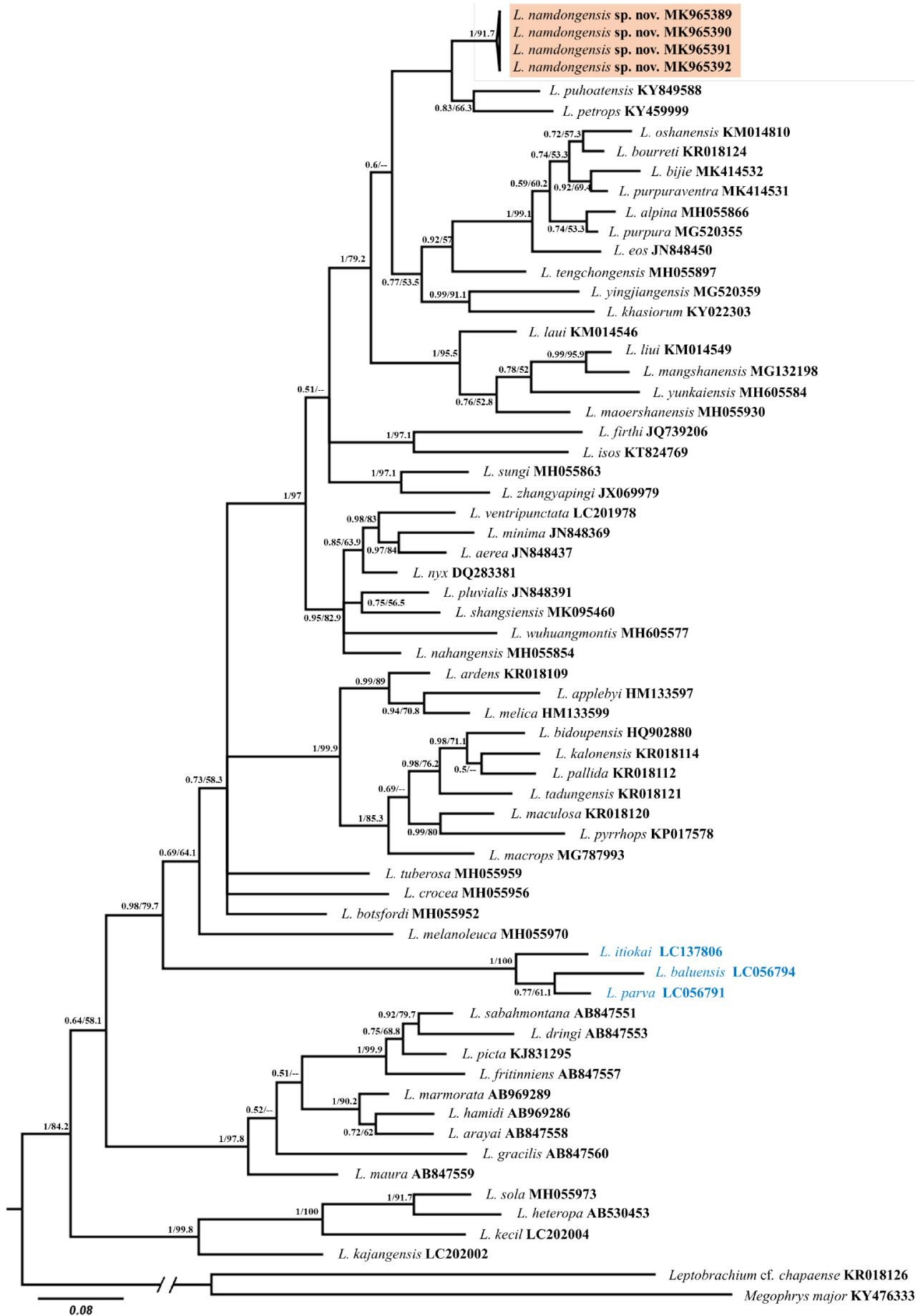


Fig. 2. The Bayesian inference (BI) tree based on the partial 16S rRNA mitochondrial gene. Values at nodes correspond to BI/ML support values, respectively. The *L. itiokai*, *L. baluensis*, and *L. parva* clade (blue) are *Leptobrachella* s.str. group. *Leptobrachium* cf. *chapaense* and *Megophrys major* are used as the outgroup.

Table 2. Selected diagnostic characters for the species in the genus *Leptobrachella* occurring north of the Isthmus of Kra (modified from Rowley et al., 2017; Yuan et al., 2017; Nguyen et al., 2018; Wang et al., 2018).

Species	Male SVL (mm)	Black Spots on Flanks	Toes Webbing	Fringes on Toes	Ventral Colouration	Dorsal Skin Texture	Distinct Dorsolateral Markings	
1. <i>L. namdongensis</i> , new species	30.9	Yes	Rudimentary	No	Creamy white with brown dusting on margins	Finely tuberculate	No	This paper
2. <i>L. aerea</i>	25.1-28.9	No	Rudimentary	Wide	Near immaculate creamy white, brown speckling on margins	Finely tuberculate	No	Rowley et al., 2010c
3. <i>L. alpina</i>	24.0-26.4	Yes	Rudimentary	Wide in males	Creamy-white with dark spots	Relatively smooth, some with small warts	Yes	Fei et al., 1990
4. <i>L. applebyi</i>	19.6-22.3	Yes	Rudimentary	No	Reddish brown with white speckling	Smooth	Yes	Rowley & Cao, 2009
5. <i>L. ardens</i>	21.3-24.7	Yes	No	No	Reddish brown with white speckling	Smooth- finely shagreened	Yes	Rowley et al., 2016
6. <i>L. bidoupensis</i>	18.5-25.4	Yes	Rudimentary	Weak	Reddish brown with white speckling	Smooth	Yes	Rowley et al., 2011
7. <i>L. botsfordi</i>	29.1-32.6	No	Rudimentary	Narrow	Reddish brown with white speckling	Shagreened	Yes	Rowley et al., 2013
8. <i>L. bourreti</i>	28.0-36.2	Yes	Rudimentary	Weak	Creamy white	Relatively smooth, some with small warts	Yes	Dubois, 1983; Ohler et al., 2011
9. <i>L. crocea</i>	22.2-27.3	No	Rudimentary	No	Bright orange	Highly tuberculate	No	Rowley et al., 2010a
10. <i>L. eos</i>	33.1-34.7	No	Rudimentary	Wide	Creamy white	Shagreened	No	Ohler et al., 2011
11. <i>L. firrhi</i>	26.4-29.2	No	Rudimentary	Wide in males	Creamy white	Shagreened with fine tubercles	No	Rowley et al., 2012
12. <i>L. fuliginosa</i>	28.2-30.0	Yes	Rudimentary	Weak	White with brown dusting	Nearly smooth, few tubercles	Yes	Matsui, 2006
13. <i>L. isos</i>	23.7-27.9	No	Rudimentary	Wide in males	Creamy white with white dusting on margins	Mostly smooth, females more tuberculate	No	Rowley, et al. 2015
14. <i>L. kalonensis</i>	25.8-30.6	Yes	No	No	Pale, speckled brown	Smooth	Yes	Rowley et al., 2016
15. <i>L. khasiorum</i>	24.5-27.3	Yes	Rudimentary	Wide	Creamy white	Isolated, scattered tubercles	Yes	Das et al., 2010
16. <i>L. lateralis</i>	26.9-28.3	Yes	Rudimentary	No	Creamy white	Roughly granular	Yes	Anderson, 1871; Humtsoe et al., 2008

Species	Male SVL (mm)	Black Spots on Flanks	Toes Webbing	Fringes on Toes	Ventral Colouration	Dorsal Skin Texture	Distinct Dorsolateral Markings
17. <i>L. laui</i>	24.8–26.7	Yes	Rudimentary	Wide	Creamy white with dark brown dusting on margins	Round granular tubercles	Yes Sung et al., 2014
18. <i>L. liui</i>	23.0–28.7	Yes	Rudimentary	Wide	Creamy white with dark brown spots on chest and margins	Round granular tubercles with glandular folds	Yes Fei et al., 1990
19. <i>L. maculosa</i>	24.2–26.6	Yes	No	No	Brown, less white speckling	Mostly smooth	Yes Rowley et al., 2016
20. <i>L. melica</i>	19.5–22.7	Yes	Rudimentary	No	Reddish brown with white speckling	Smooth	Yes Rowley et al., 2010b
21. <i>L. minima</i>	25.7–31.4	Yes	Rudimentary	No	Creamy white	Smooth	Yes Ohler et al., 2011; Taylor, 1962
22. <i>L. nahangensis</i>	40.8	Yes	Rudimentary	No	Creamy white with light speckling on throat and chest	Smooth	Yes Lathrop et al., 1998
23. <i>L. nokrekensis</i>	26.0–33.0	Yes	Rudimentary	unknown	Creamy white	Tubercles and longitudinal folds	Yes Mathew & Sen, 2010
24. <i>L. nyx</i>	26.7–32.6	Yes	Rudimentary	No	Creamy white with white with brown margins	Rounded tubercles	Yes Ohler et al., 2011
25. <i>L. oshanensis</i>	26.6–30.7	Yes	No	No	Whitish with no markings or only small, light grey spots	Smooth with few glandular ridges	Yes Liu, 1950; Fei et al., 2009, 2012
26. <i>L. pallida</i>	24.5–27.7	No	No	No	Reddish brown with white speckling	Tuberculate	No Rowley et al., 2016
27. <i>L. pelodytoides</i>	27.5–32.3	Yes	Wide	Narrow	Whitish	Small, smooth warts	Yes Boulenger, 1893; Ohler et al., 2011
28. <i>L. petrops</i>	23.6–27.6	No	No	Narrow	Immaculate creamy white	Highly tuberculate	No Rowley et al., 2017b
29. <i>L. pluvialis</i>	21.3–22.3	Yes	Rudimentary	No	Dirty white with dark brown marbling	Smooth, flattened tubercles on flanks	Yes Ohler et al., 2000
30. <i>L. pulhoatensis</i>	24.2–28.1	Yes	Rudimentary	Narrow	Reddish brown with white dusting	Longitudinal skin ridges	Yes Rowley et al., 2017a
31. <i>L. pyrrhops</i>	30.8–34.3	Yes	Rudimentary	No	Reddish brown with white speckling	Slightly shagreened	Yes Poyarkov et al., 2015
32. <i>L. rowleyae</i>	23.4–25.4	Yes	Rudimentary	No	pinkish milk-white with dense whitish speckling evenly scattered on entire ventral surface	mostly smooth with numerous tiny tubercles and pustules finely	No Nguyen et al., 2018
33. <i>L. sungi</i>	48.3–52.7	No or small	Wide	Weak	White	Granular	Yes Lathrop et al., 1998

Species	Male SVL (mm)	Black Spots on Flanks	Toes Webbing	Fringes on Toes	Ventral Colouration	Dorsal Skin Texture	Distinct Dorsolateral Markings
34. <i>L. tadungensis</i>	23.3–28.2	Yes	No	No	Reddish brown with white speckling	Smooth	Yes
35. <i>L. tamdil</i>	32.3	Yes	Wide	Wide	White	Weakly tuberculate	Yes
36. <i>L. tengchongensis</i>	23.9–26.0	Yes	Rudimentary	Narrow	White with dark brown blotches	Shagreened with small tubercles	Yes
37. <i>L. tuberosa</i>	24.4–29.5	No	Rudimentary	No	White with small grey spots/streaks	Highly tuberculate	No
38. <i>L. ventripunctata</i>	25.5–28.0	Yes	Rudimentary	No	Chest and belly with dark brown spots	Longitudinal skin ridges	Yes
39. <i>L. wuhuangmonitis</i>	25.6–30.0	Yes	Rudimentary	Narrow	Greyish white mixed by tiny white and black dots	Rough, scattered with dense conical tubercles	No
40. <i>L. yunkaiensis</i>	25.9–29.3	Yes	Rudimentary	Wide	Belly pinkish with distinct or indistinct speckling	Shagreened with fine tubercles and short skin ridges	No
41. <i>L. zhangyapingi</i>	45.8–52.5	No	Rudimentary	Wide	Creamy-white with white with brown margins	Mostly smooth with distinct tubercles	Weak

al. (2017a): Measurements included snout-vent length (SVL); head length from tip of snout to rear of jaws (HDL); head width at commissure of jaws (HDW); snout length from tip of snout to anterior corner of eye (SNT); diameter of exposed portion of eyeball (EYE); interorbital distance (IOD); horizontal diameter of tympanum (TMP); distance from anterior edge of tympanum to posterior corner of eye (TEY); tibia length with hindlimb flexed (TIB); distance from nostril to anterior edge of eye (EN); distance between nostrils (IN); distance from nostril to tip of snout (NS); manus length from tip of third digit to proximal edge of inner palmar tubercle (ML); pes length from tip of fourth toe to proximal edge of the inner metatarsal tubercle (PL); and length of fingers 1–3 from tip to the distal edge of the inner palmar tubercle (F1–3).

## RESULTS

**Molecular phylogenetic analysis.** The 16S rRNA dataset contained 63 individuals from 60 species in the ingroup and two species for the outgroup with 547 bp in the final alignment. Among the 547 sites, 261 sites were conserved and 280 sites were variable, of which 216 were found to be potentially parsimony-informative. The transition–transversion bias was estimated as 1.8. Nucleotide frequencies were A=31.16%, T=22.79%, C=25.30%, and G=20.75%. The ML and Bayesian analyses produced topologies with  $-\ln L = 7815.6138$  and  $7763.0781$ , respectively. The best model selected for ML was the general time reversible model (GTR: Tavaré, 1986) with a gamma shape parameter (G: 0.251 in ML and 0.267 in BI). Phylogenetic analyses employing ML and BI methods were near-identical, with most well-supported nodes on the ML tree also being well-supported on the Bayesian tree, and only the BI tree is presented in Fig. 2. In both analyses, the newly collected *Leptobranchella* specimens were recovered as sister to *L. petrops* and *L. puhoatensis*, recently described from northern Vietnam (Rowley et al., 2017b, 2017a).

Interspecific uncorrected p-distances of the *Leptobranchella* (Table 3) ranged from 1.6% (between *L. liui* and *L. mangshanensis*) to 24% (between *L. liui* and *L. gracilis*). The genetic divergence of the unidentified species from Nam Dong NR and its congeners ranged from 4.7% (*L. puhoatensis*) to 21.0% (*L. gracilis*), which was higher than genetic distances between some other recognised species of *Leptobranchella* (4.6% between *L. marmorata* and *L. hamidi*, *L. arayai* and *L. hamidi*, *L. nahangensis* and *L. aerea*; 4.3% between *L. aerea* and *L. nyx*, *L. pluvialis* and *L. aerea*, *L. baluensis* and *L. parva*; 4.0% between *L. picta* and *L. sabahmontana*; 3.6% between *L. alpina*



Table 3. Uncorrected (“p”) distance matrix showing percentage pair wise genetic divergence 16S between members of the *Leptobranchella* species group.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
1 <i>Leptobranchella namdongensis</i> , new species																							
2 <i>Leptobranchella namdongensis</i> , new species	0.000																						
3 <i>Leptobranchella namdongensis</i> , new species	0.000	0.000																					
4 <i>Leptobranchella namdongensis</i> , new species	0.000	0.000	0.000																				
5 <i>Leptobranchella pulicatensis</i>	0.047	0.047	0.047	0.047																			
6 <i>Leptobranchella petrops</i>	0.068	0.068	0.068	0.068	0.064																		
7 <i>Leptobranchella laui</i>	0.075	0.075	0.075	0.075	0.089	0.083																	
8 <i>Leptobranchella liui</i>	0.094	0.094	0.094	0.094	0.094	0.091	0.057																
9 <i>Leptobranchella oshamensis</i>	0.086	0.086	0.086	0.086	0.097	0.101	0.071	0.078															
10 <i>Leptobranchella eos</i>	0.094	0.094	0.094	0.094	0.108	0.105	0.096	0.078	0.047														
11 <i>Leptobranchella ventripunctata</i>	0.087	0.087	0.087	0.087	0.099	0.099	0.090	0.095	0.101	0.117													
12 <i>Leptobranchella minima</i>	0.087	0.087	0.087	0.087	0.095	0.110	0.075	0.079	0.083	0.109	0.072												
13 <i>Leptobranchella aerea</i>	0.097	0.097	0.097	0.097	0.108	0.102	0.085	0.079	0.089	0.108	0.068	0.061											
14 <i>Leptobranchella bourreti</i>	0.090	0.090	0.090	0.090	0.090	0.105	0.081	0.074	0.030	0.033	0.101	0.090	0.085										
15 <i>Leptobranchella nyx</i>	0.083	0.083	0.083	0.083	0.087	0.095	0.075	0.068	0.072	0.090	0.058	0.054	0.043	0.075									
16 <i>Leptobranchella pluvialis</i>	0.106	0.106	0.106	0.106	0.106	0.101	0.082	0.076	0.090	0.105	0.072	0.061	0.043	0.082	0.047								
17 <i>Leptobranchella firithi</i>	0.118	0.118	0.118	0.118	0.122	0.138	0.120	0.112	0.124	0.132	0.106	0.118	0.116	0.120	0.094	0.121							

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
18 <i>Leptobranchella isos</i>	0.113	0.113	0.113	0.113	0.129	0.130	0.123	0.119	0.113	0.125	0.109	0.128	0.119	0.105	0.112	0.140	0.118						
19 <i>Leptobranchella ardens</i>	0.172	0.172	0.172	0.172	0.157	0.168	0.162	0.164	0.145	0.160	0.157	0.160	0.139	0.136	0.135	0.141	0.183	0.148					
20 <i>Leptobranchella applebyi</i>	0.156	0.156	0.156	0.156	0.161	0.170	0.151	0.153	0.145	0.148	0.153	0.137	0.131	0.136	0.124	0.137	0.170	0.144	0.064				
21 <i>Leptobranchella melica</i>	0.156	0.156	0.156	0.156	0.149	0.175	0.171	0.160	0.153	0.156	0.149	0.140	0.119	0.136	0.112	0.133	0.174	0.147	0.053	0.057			
22 <i>Leptobranchella bidoupensis</i>	0.174	0.174	0.174	0.174	0.167	0.181	0.180	0.154	0.182	0.165	0.177	0.166	0.155	0.169	0.144	0.154	0.181	0.144	0.100	0.082	0.078		
23 <i>Leptobranchella kalomensis</i>	0.187	0.187	0.187	0.187	0.171	0.181	0.185	0.162	0.174	0.165	0.179	0.175	0.156	0.164	0.145	0.149	0.191	0.174	0.108	0.113	0.112	0.054	
24 <i>Leptobranchella pallida</i>	0.183	0.183	0.183	0.183	0.179	0.169	0.177	0.163	0.162	0.162	0.178	0.157	0.156	0.165	0.153	0.146	0.195	0.173	0.097	0.098	0.104	0.057	
25 <i>Leptobranchella tadungensis</i>	0.152	0.152	0.152	0.152	0.145	0.157	0.155	0.129	0.160	0.164	0.157	0.145	0.131	0.155	0.129	0.133	0.161	0.144	0.093	0.097	0.104	0.057	
26 <i>Leptobranchella maculosa</i>	0.154	0.154	0.154	0.154	0.139	0.150	0.161	0.142	0.150	0.161	0.159	0.158	0.133	0.141	0.129	0.138	0.162	0.157	0.075	0.097	0.100	0.085	
27 <i>Leptobranchella pyrrhops</i>	0.170	0.170	0.170	0.170	0.171	0.158	0.164	0.158	0.161	0.166	0.161	0.166	0.144	0.164	0.153	0.153	0.182	0.156	0.090	0.128	0.124	0.094	
28 <i>Leptobranchella sabahmontana</i>	0.163	0.163	0.163	0.163	0.172	0.182	0.175	0.178	0.178	0.170	0.158	0.163	0.164	0.168	0.157	0.171	0.183	0.182	0.157	0.130	0.138	0.142	
29 <i>Leptobranchella dringi</i>	0.168	0.168	0.168	0.168	0.168	0.166	0.172	0.173	0.174	0.174	0.162	0.167	0.152	0.164	0.153	0.167	0.183	0.187	0.164	0.162	0.161	0.157	
30 <i>Leptobranchella picta</i>	0.172	0.172	0.172	0.172	0.177	0.187	0.189	0.183	0.187	0.184	0.166	0.171	0.160	0.174	0.154	0.168	0.166	0.187	0.157	0.155	0.154	0.158	
31 <i>Leptobranchella gracilis</i>	0.210	0.210	0.210	0.210	0.202	0.225	0.196	0.223	0.190	0.212	0.203	0.194	0.180	0.189	0.193	0.183	0.213	0.195	0.145	0.154	0.154	0.176	
32 <i>Leptobranchella marmorata</i>	0.147	0.147	0.147	0.147	0.155	0.161	0.156	0.162	0.162	0.142	0.146	0.161	0.144	0.138	0.145	0.159	0.175	0.154	0.128	0.114	0.133	0.150	
33 <i>Leptobranchella hamidi</i>	0.166	0.166	0.166	0.166	0.171	0.165	0.171	0.178	0.178	0.154	0.154	0.172	0.163	0.165	0.156	0.170	0.187	0.157	0.139	0.132	0.132	0.149	
34 <i>Leptobranchella arayai</i>	0.154	0.154	0.154	0.154	0.146	0.165	0.164	0.167	0.170	0.158	0.134	0.153	0.152	0.146	0.145	0.159	0.179	0.149	0.121	0.114	0.125	0.149	
35 <i>Leptobranchella bijje</i>	0.101	0.101	0.101	0.101	0.115	0.124	0.090	0.093	0.061	0.071	0.109	0.109	0.097	0.057	0.093	0.112	0.135	0.143	0.164	0.152	0.156	0.176	
36 <i>Leptobranchella purpuraventra</i>	0.082	0.082	0.082	0.082	0.089	0.089	0.093	0.079	0.047	0.047	0.090	0.097	0.082	0.026	0.079	0.083	0.132	0.121	0.132	0.132	0.124	0.164	
37 <i>Leptobranchella shangsiensis</i>	0.109	0.109	0.109	0.109	0.106	0.121	0.090	0.087	0.093	0.108	0.076	0.072	0.061	0.093	0.054	0.047	0.133	0.140	0.157	0.157	0.145	0.171	

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
38 <i>Leptobrachella yunkaiensis</i>	0.101	0.101	0.101	0.101	0.104	0.113	0.053	0.060	0.082	0.104	0.113	0.093	0.100	0.085	0.090	0.087	0.131	0.119	0.177	0.157	0.172	0.162
39 <i>Leptobrachella wuhuangmontis</i>	0.128	0.128	0.128	0.128	0.117	0.144	0.111	0.094	0.097	0.112	0.083	0.098	0.068	0.090	0.068	0.072	0.127	0.115	0.133	0.136	0.132	0.144
40 <i>Leptobrachella sola</i>	0.206	0.206	0.206	0.206	0.214	0.231	0.220	0.196	0.196	0.205	0.201	0.214	0.175	0.187	0.185	0.187	0.218	0.203	0.186	0.178	0.209	0.206
41 <i>Leptobrachella fritiniensis</i>	0.177	0.177	0.177	0.177	0.176	0.171	0.182	0.176	0.175	0.172	0.159	0.176	0.153	0.166	0.154	0.160	0.184	0.176	0.161	0.175	0.166	0.142
42 <i>Leptobrachella melanoleuca</i>	0.121	0.121	0.121	0.121	0.116	0.126	0.154	0.147	0.124	0.135	0.124	0.128	0.104	0.116	0.101	0.108	0.168	0.156	0.128	0.132	0.123	0.148
43 <i>Leptobrachella tuberosa</i>	0.117	0.117	0.117	0.117	0.117	0.129	0.123	0.120	0.113	0.109	0.105	0.113	0.111	0.105	0.093	0.113	0.140	0.094	0.131	0.128	0.131	0.114
44 <i>Leptobrachella crocea</i>	0.141	0.141	0.141	0.141	0.129	0.147	0.139	0.140	0.141	0.128	0.145	0.133	0.116	0.125	0.120	0.121	0.153	0.153	0.124	0.113	0.120	0.106
45 <i>Leptobrachella boisfordi</i>	0.102	0.102	0.102	0.102	0.098	0.116	0.105	0.105	0.116	0.115	0.110	0.114	0.101	0.112	0.094	0.106	0.133	0.137	0.125	0.121	0.132	0.133
46 <i>Leptobrachella maoershanensis</i>	0.097	0.097	0.097	0.097	0.111	0.093	0.053	0.061	0.096	0.107	0.089	0.092	0.075	0.099	0.082	0.082	0.147	0.119	0.147	0.136	0.155	0.157
47 <i>Leptobrachella tengchongensis</i>	0.072	0.072	0.072	0.072	0.079	0.065	0.075	0.078	0.079	0.082	0.094	0.072	0.082	0.075	0.072	0.094	0.114	0.102	0.154	0.151	0.142	0.164
48 <i>Leptobrachella alpina</i>	0.090	0.090	0.090	0.090	0.097	0.100	0.085	0.089	0.047	0.047	0.113	0.112	0.089	0.033	0.086	0.090	0.128	0.124	0.143	0.136	0.136	0.159
49 <i>Leptobrachella sungi</i>	0.091	0.091	0.091	0.091	0.095	0.106	0.101	0.094	0.090	0.105	0.086	0.083	0.074	0.093	0.068	0.072	0.110	0.128	0.173	0.156	0.160	0.150
50 <i>Leptobrachella macrops</i>	0.169	0.169	0.169	0.169	0.162	0.165	0.172	0.150	0.165	0.164	0.178	0.161	0.144	0.156	0.148	0.153	0.186	0.153	0.075	0.097	0.085	0.078
51 <i>Leptobrachella yingjiangensis</i>	0.105	0.105	0.105	0.105	0.101	0.082	0.082	0.083	0.097	0.086	0.122	0.109	0.116	0.086	0.109	0.105	0.153	0.133	0.150	0.147	0.150	0.144
52 <i>Leptobrachella purpura</i>	0.086	0.086	0.086	0.086	0.100	0.093	0.085	0.075	0.047	0.026	0.106	0.105	0.089	0.033	0.079	0.090	0.124	0.121	0.151	0.136	0.143	0.152
53 <i>Leptobrachella mangshanensis</i>	0.090	0.090	0.090	0.090	0.097	0.090	0.054	0.016	0.082	0.097	0.099	0.083	0.079	0.085	0.072	0.076	0.116	0.123	0.157	0.145	0.161	0.154
54 <i>Leptobrachella keel</i>	0.203	0.203	0.203	0.203	0.194	0.200	0.231	0.207	0.199	0.194	0.199	0.207	0.189	0.185	0.184	0.188	0.240	0.190	0.163	0.168	0.176	0.177
55 <i>Leptobrachella kajangensis</i>	0.157	0.157	0.157	0.157	0.161	0.181	0.162	0.160	0.160	0.164	0.156	0.172	0.131	0.151	0.146	0.145	0.181	0.148	0.113	0.113	0.144	0.129
56 <i>Leptobrachella ittokai</i>	0.179	0.179	0.179	0.179	0.172	0.171	0.204	0.188	0.201	0.204	0.171	0.193	0.174	0.183	0.171	0.172	0.193	0.191	0.175	0.158	0.183	0.180

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
57	<i>Leptobranchella batuensis</i>	0.181	0.181	0.181	0.166	0.164	0.200	0.168	0.182	0.185	0.160	0.195	0.163	0.161	0.160	0.157	0.186	0.173	0.142	0.157	0.162	0.158
58	<i>Leptobranchella khasiorum</i>	0.109	0.109	0.109	0.101	0.112	0.097	0.086	0.119	0.108	0.149	0.120	0.135	0.108	0.113	0.120	0.130	0.165	0.173	0.153	0.162	0.164
59	<i>Leptobranchella parva</i>	0.169	0.169	0.169	0.175	0.162	0.185	0.170	0.195	0.198	0.161	0.183	0.165	0.178	0.162	0.155	0.187	0.169	0.157	0.165	0.182	0.170
60	<i>Leptobranchella zhangvapingi</i>	0.106	0.106	0.106	0.113	0.117	0.097	0.104	0.089	0.093	0.109	0.108	0.100	0.092	0.086	0.097	0.125	0.125	0.164	0.147	0.163	0.169
61	<i>Leptobranchella maura</i>	0.141	0.141	0.141	0.141	0.160	0.171	0.165	0.166	0.169	0.145	0.156	0.147	0.157	0.145	0.154	0.174	0.145	0.132	0.124	0.133	0.145
62	<i>Leptobranchella nahangensis</i>	0.076	0.076	0.076	0.072	0.095	0.082	0.075	0.075	0.093	0.068	0.058	0.046	0.075	0.030	0.047	0.094	0.108	0.136	0.136	0.117	0.141
63	<i>Leptobranchella heteropa</i>	0.205	0.205	0.205	0.196	0.202	0.207	0.208	0.208	0.217	0.180	0.186	0.161	0.195	0.160	0.170	0.220	0.204	0.182	0.153	0.166	0.189
64	<i>Leptobranchium cf. chapaense</i>	0.234	0.234	0.234	0.252	0.222	0.263	0.269	0.261	0.280	0.247	0.268	0.264	0.265	0.257	0.255	0.307	0.274	0.251	0.264	0.290	0.289
65	<i>Megophrys major</i>	0.282	0.282	0.282	0.291	0.288	0.289	0.296	0.268	0.279	0.274	0.311	0.282	0.270	0.282	0.285	0.313	0.272	0.267	0.268	0.298	0.304
24	<i>Leptobranchella pallida</i>	0.058																				
25	<i>Leptobranchella tadungensis</i>	0.065	0.072																			
26	<i>Leptobranchella maculosa</i>	0.089	0.089	0.075																		
27	<i>Leptobranchella pyrrhops</i>	0.091	0.076	0.076	0.071																	
28	<i>Leptobranchella sabahmontana</i>	0.142	0.141	0.141	0.153	0.162																
29	<i>Leptobranchella dringi</i>	0.161	0.157	0.157	0.166	0.165	0.053															
30	<i>Leptobranchella picta</i>	0.158	0.158	0.153	0.162	0.170	0.040	0.053														
31	<i>Leptobranchella gracilis</i>	0.189	0.167	0.187	0.180	0.175	0.123	0.120														

	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	
32	<i>Leptobrachella marmorata</i>	0.163	0.146	0.157	0.150	0.163	0.097	0.093	0.090	0.108													
33	<i>Leptobrachella hamidi</i>	0.174	0.161	0.178	0.178	0.174	0.101	0.108	0.101	0.112	0.046												
34	<i>Leptobrachella arayai</i>	0.155	0.138	0.162	0.154	0.166	0.101	0.108	0.094	0.116	0.033	0.046											
35	<i>Leptobrachella bijie</i>	0.176	0.173	0.162	0.169	0.198	0.208	0.195	0.208	0.225	0.169	0.193	0.169										
36	<i>Leptobrachella purpuraventra</i>	0.160	0.156	0.160	0.145	0.165	0.185	0.177	0.186	0.202	0.141	0.164	0.137	0.047									
37	<i>Leptobrachella shangsiensis</i>	0.158	0.167	0.150	0.162	0.162	0.173	0.173	0.179	0.195	0.163	0.167	0.163	0.124	0.097								
38	<i>Leptobrachella yunkaiensis</i>	0.182	0.166	0.141	0.154	0.165	0.185	0.190	0.200	0.201	0.166	0.193	0.169	0.112	0.097	0.105							
39	<i>Leptobrachella wuhuangmontis</i>	0.153	0.157	0.140	0.129	0.153	0.173	0.173	0.181	0.199	0.153	0.165	0.145	0.119	0.101	0.083	0.112						
40	<i>Leptobrachella sola</i>	0.220	0.206	0.188	0.189	0.175	0.198	0.189	0.184	0.221	0.184	0.209	0.201	0.213	0.197	0.218	0.200	0.170					
41	<i>Leptobrachella frittimiens</i>	0.158	0.150	0.134	0.170	0.158	0.067	0.067	0.053	0.128	0.097	0.083	0.101	0.192	0.179	0.167	0.188	0.170	0.189				
42	<i>Leptobrachella melanoleuca</i>	0.160	0.144	0.137	0.149	0.157	0.145	0.149	0.157	0.169	0.151	0.158	0.139	0.134	0.107	0.128	0.167	0.131	0.200	0.153			
43	<i>Leptobrachella tuberosa</i>	0.126	0.125	0.113	0.124	0.117	0.133	0.137	0.145	0.153	0.117	0.125	0.125	0.139	0.127	0.117	0.127	0.112	0.192	0.122	0.109		
44	<i>Leptobrachella crocea</i>	0.122	0.122	0.128	0.144	0.145	0.153	0.141	0.141	0.149	0.129	0.144	0.137	0.132	0.124	0.141	0.156	0.129	0.193	0.149	0.131	0.101	
45	<i>Leptobrachella boisfordi</i>	0.141	0.138	0.120	0.134	0.146	0.137	0.126	0.142	0.158	0.125	0.140	0.129	0.135	0.115	0.121	0.124	0.121	0.181	0.138	0.090	0.084	0.102
46	<i>Leptobrachella maershanensis</i>	0.169	0.169	0.136	0.146	0.149	0.168	0.172	0.181	0.209	0.145	0.163	0.156	0.112	0.096	0.100	0.071	0.108	0.196	0.174	0.150	0.119	0.135
47	<i>Leptobrachella tengchongensis</i>	0.164	0.165	0.152	0.149	0.165	0.177	0.162	0.170	0.210	0.145	0.152	0.144	0.096	0.074	0.097	0.100	0.119	0.218	0.163	0.130	0.101	0.131
48	<i>Leptobrachella alpinu</i>	0.171	0.167	0.155	0.141	0.176	0.172	0.172	0.182	0.193	0.145	0.156	0.160	0.050	0.036	0.104	0.093	0.108	0.192	0.158	0.126	0.119	0.124

	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	
49	<i>Leptobrachella sungi</i>	0.162	0.171	0.145	0.155	0.173	0.175	0.171	0.212	0.150	0.173	0.161	0.108	0.097	0.094	0.101	0.105	0.191	0.172	0.135	0.125	0.149	
50	<i>Leptobrachella macrops</i>	0.079	0.075	0.072	0.068	0.079	0.146	0.162	0.154	0.138	0.140	0.137	0.184	0.152	0.158	0.177	0.157	0.215	0.159	0.152	0.136	0.128	
51	<i>Leptobrachella yingiangensis</i>	0.148	0.144	0.143	0.144	0.141	0.178	0.177	0.178	0.214	0.145	0.148	0.108	0.093	0.125	0.090	0.143	0.213	0.179	0.150	0.120	0.112	
52	<i>Leptobrachella purpura</i>	0.155	0.152	0.140	0.148	0.161	0.169	0.169	0.178	0.214	0.137	0.156	0.054	0.036	0.097	0.093	0.108	0.196	0.154	0.126	0.097	0.119	
53	<i>Leptobrachella mangshanensis</i>	0.162	0.163	0.129	0.135	0.158	0.178	0.174	0.183	0.215	0.162	0.177	0.166	0.097	0.091	0.057	0.094	0.193	0.176	0.148	0.121	0.140	
54	<i>Leptobrachella kecil</i>	0.212	0.190	0.182	0.198	0.185	0.191	0.197	0.203	0.222	0.198	0.209	0.197	0.220	0.172	0.215	0.202	0.177	0.101	0.216	0.170	0.190	0.200
55	<i>Leptobrachella kajangensis</i>	0.158	0.154	0.133	0.134	0.136	0.149	0.152	0.156	0.142	0.118	0.140	0.176	0.152	0.172	0.144	0.140	0.117	0.149	0.139	0.137	0.141	
56	<i>Leptobrachella itokai</i>	0.193	0.183	0.179	0.164	0.197	0.198	0.190	0.203	0.214	0.181	0.206	0.181	0.200	0.182	0.198	0.195	0.175	0.206	0.211	0.182	0.176	0.179
57	<i>Leptobrachella baluensis</i>	0.159	0.171	0.154	0.155	0.167	0.163	0.155	0.175	0.154	0.170	0.155	0.189	0.164	0.182	0.176	0.164	0.191	0.162	0.176	0.153	0.157	
58	<i>Leptobrachella khaistorum</i>	0.180	0.176	0.158	0.172	0.167	0.176	0.163	0.176	0.201	0.151	0.162	0.138	0.119	0.140	0.112	0.144	0.206	0.193	0.151	0.145	0.114	
59	<i>Leptobrachella parva</i>	0.176	0.174	0.166	0.159	0.179	0.179	0.164	0.176	0.187	0.170	0.191	0.179	0.199	0.177	0.188	0.169	0.182	0.179	0.184	0.185	0.158	0.178
60	<i>Leptobrachella zhangyapingi</i>	0.172	0.181	0.168	0.149	0.168	0.178	0.186	0.178	0.206	0.165	0.177	0.104	0.096	0.112	0.123	0.127	0.195	0.187	0.142	0.123	0.151	
61	<i>Leptobrachella maura</i>	0.175	0.145	0.148	0.158	0.182	0.094	0.101	0.105	0.105	0.089	0.089	0.160	0.149	0.178	0.172	0.161	0.178	0.108	0.136	0.125	0.125	
62	<i>Leptobrachella nahangensis</i>	0.150	0.149	0.129	0.126	0.141	0.146	0.142	0.150	0.169	0.133	0.144	0.104	0.086	0.061	0.090	0.065	0.166	0.154	0.097	0.090	0.109	
63	<i>Leptobrachella heteropa</i>	0.208	0.198	0.189	0.202	0.180	0.206	0.189	0.197	0.208	0.176	0.179	0.180	0.212	0.191	0.188	0.203	0.170	0.061	0.190	0.181	0.180	0.182
64	<i>Leptobrachium cf. chapense</i>	0.295	0.265	0.278	0.258	0.240	0.303	0.287	0.286	0.288	0.259	0.244	0.284	0.245	0.290	0.275	0.262	0.260	0.297	0.231	0.268	0.243	
65	<i>Megophrys major</i>	0.298	0.329	0.284	0.290	0.299	0.292	0.292	0.293	0.272	0.263	0.265	0.271	0.279	0.325	0.304	0.286	0.291	0.292	0.291	0.288	0.299	

	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	
46	<i>Leptobrachella maershanensis</i>	0.104																				
47	<i>Leptobrachella tengchongensis</i>	0.101	0.103																			
48	<i>Leptobrachella alpinu</i>	0.115	0.096	0.085																		
49	<i>Leptobrachella sungi</i>	0.116	0.104	0.079	0.105																	
50	<i>Leptobrachella macrops</i>	0.156	0.145	0.160	0.163	0.174																
51	<i>Leptobrachella yingjiangensis</i>	0.128	0.101	0.086	0.089	0.125	0.147															
52	<i>Leptobrachella purpura</i>	0.119	0.089	0.078	0.020	0.094	0.155	0.082														
53	<i>Leptobrachella mangshanensis</i>	0.106	0.054	0.090	0.086	0.098	0.150	0.094	0.079													
54	<i>Leptobrachella kecil</i>	0.190	0.206	0.205	0.180	0.196	0.207	0.202	0.184	0.208												
55	<i>Leptobrachella kajangensis</i>	0.125	0.136	0.176	0.148	0.156	0.156	0.177	0.160	0.153	0.124											
56	<i>Leptobrachella itokai</i>	0.178	0.196	0.187	0.186	0.172	0.196	0.196	0.182	0.183	0.231	0.183										
57	<i>Leptobrachella bahuensis</i>	0.148	0.184	0.168	0.171	0.146	0.179	0.185	0.168	0.164	0.212	0.173	0.082									
58	<i>Leptobrachella khasiorum</i>	0.114	0.119	0.108	0.119	0.128	0.175	0.090	0.119	0.105	0.198	0.182	0.213	0.197								
59	<i>Leptobrachella parva</i>	0.153	0.177	0.169	0.184	0.147	0.187	0.195	0.181	0.165	0.208	0.161	0.057	0.043	0.207							
60	<i>Leptobrachella zhangyapingi</i>	0.128	0.104	0.089	0.078	0.061	0.168	0.116	0.078	0.101	0.190	0.159	0.182	0.163	0.139	0.169						
61	<i>Leptobrachella maura</i>	0.145	0.160	0.164	0.145	0.162	0.153	0.173	0.156	0.169	0.165	0.109	0.170	0.153	0.158	0.157	0.162					
62	<i>Leptobrachella nahangensis</i>	0.083	0.085	0.082	0.086	0.064	0.141	0.102	0.089	0.079	0.170	0.136	0.171	0.157	0.098	0.162	0.089	0.129				
63	<i>Leptobrachella heteropa</i>	0.178	0.194	0.195	0.200	0.191	0.214	0.208	0.208	0.205	0.119	0.132	0.221	0.202	0.191	0.211	0.199	0.181	0.165			
64	<i>Leptobrachium cf. chapaense</i>	0.238	0.254	0.266	0.277	0.259	0.260	0.254	0.273	0.265	0.273	0.250	0.267	0.279	0.245	0.266	0.295	0.239	0.233	0.282		
65	<i>Megophrys major</i>	0.285	0.281	0.289	0.275	0.288	0.329	0.288	0.284	0.303	0.328	0.246	0.292	0.254	0.280	0.278	0.312	0.246	0.289	0.272	0.304	



Fig. 3. Dorsolateral view (A) and ventral view (B) of the holotype (VNUF A.2017.37, male) of *Leptobrachella namdongensis*, new species in life. Photos by Vinh Q. Luu.

and *L. purpuraventra*, *L. purpura* and *L. purpuraventra*; 3.3% between *L. eos* and *L. bourreti*, *L. marmorata* and *L. arayai*, *L. alpina* and *L. bourreti*, *L. purpura* and *L. bourreti*; 3.0% between *L. oshanensis* and *L. bourreti*, *L. nyx* and *L. nahangensis*; 2.6% between *L. purpuraventra* and *L. bourreti*, *L. eos* and *L. purpura*; 2.0% between *L. alpina* and *L. purpura*; 1.6% between *L. liui* and *L. mangshanensis*), (Table 3), indicating that the differentiations between the new form and its congeners has reached specific level.

**Morphological systematics analysis.** The unidentified species differs from all compared species of *Leptobrachella* recorded to the north of the Isthmus of Kra by the body size, the presence black spots on flanks, the absence of distinct blackish dorsolateral markings (canthal stripe and/or lateral blotches), the absence of fringes on toes, toe webbing formula, ventral colouration, and dorsal skin texture (Table 2).

The results of both the phylogenetic analyses and genetic distances support the unidentified species as being most closely related to *L. puhoatensis* and *L. petrops* (Fig. 2, Table 3). The new population differs from those two species by having a creamy white venter with brown dots on the outer margins of the throat and belly (vs. a reddish-brown venter in males and a pale pink venter in females of *L. puhoatensis*; a translucent white throat in males of *L. petrops*); dorsal skin with fine tubercles (vs. longitudinal skin ridges in *L. puhoatensis*; densely tuberculate skin texture in *L. petrops*); head wider than long (head longer than wide in *L. puhoatensis* and *L. petrops*); the absence of black markings on the head (vs. present in *L. puhoatensis*).

In addition, the unidentified species has a distinct tympanum that diagnoses it from *L. crocea* and *L. tuberosa* (hidden tympanum); head wider than long (vs. head longer than wide in *L. aerea*, *L. bidoupensis*, *L. rowleyae*, *L. isos*, *L. pyrrhops*, *L. laui*, *L. ventripunctata*, *L.oes*, *L. nyx*, and *L. sabahmontana*). The new species, has a bicoloured iris with

a copper upper half and can be distinguished from other species with a uniformly coloured iris, such as: *L. aerea* (bronze iris), *L. botsfordi* (brownish golden iris), *L. firthi* (bright golden iris), *L. pluvialis* (dark golden iris), *L. sungi* (golden green iris), and *L. tuberosa* (golden iris).

#### *Leptobrachella namdongensis*, new species

(Figs. 3–5; Tables 2, 4)

**Holotype.** Adult male VNUF A.2017.37 (field number: ND2.17.37), VIETNAM: Thanh Hoa Province, Quan Hoa District, Nam Dong Commune, Nam Dong Conservation Area, 20°19'44.9"N, 104°55'05.7"E, 710 m a.s.l., in evergreen forest, Q.V. Luu et al. Coll., 13 July 2017.

**Paratypes (n=6).** Three adult females VNMN2019.04 (field number: ND.17.0176); IEBR 4512 (ND.17.0179); VNUF A.2017.95 (field number: ND.17.95), VIETNAM: Thanh Hoa Province, Quan Hoa District, Nam Dong Commune, Nam Dong Conservation Area, 20°19'17.3"N, 104°55'15.6"E, 740 m a.s.l., in evergreen forest, Q.V. Luu et al. Coll., 30 May 2017. Three adult females VNUF A.2018.15 (field number: ND.18.15); VNMN2019.05 (field number: ND.18.14); IEBR 4513 (field number: ND.18.08), VIETNAM: Thanh Hoa Province, Quan Son District, Trung Thuong Commune, Nam Dong Conservation Area, 20°18'211"N, 104°54'349"E, 589 m a.s.l., in evergreen forest, Q.V. Luu et al. Coll. 14 April 2018.

**Diagnosis.** *Leptobrachella namdongensis*, new species is distinguished from its congeners by a combination of the following morphological characters: size medium (30.9 mm in the adult male and 32.1–35.3 mm in adult females); head wider than long; tympanum distinct; throat immaculate white, chest and belly with dark speckling on outer margins; toes with basal webbing and without lateral fringe; supratympanic fold edged by a distinct black line; inter-orbital region with



Table 4. Measurements (in mm) and proportions of the type series of *Leptobranchella namdongensis*, new species (H = Holotype, P = Paratype, for other abbreviations see Material & Methods).

Specimen ID	VNUF A.2017.37		VNUF A.2017.95		VNMIN 2019.04		IEBR 4512		VNUF A.2018.15		VNMIN 2019.05		IEBR 4513	
	H	P	Female	P	Female	P	Female	P	Female	P	Female	P	Female	P
Type status														
Sex	Male		Female		Female		Female		Female		Female		Female	
SVL	30.9		32.1		33.0		32.7		32.2		32.6		35.3	
HDL	10.6		9.8		10.6		10.2		10.6		10.2		11.3	
HDW	11.5		10.8		11.5		11.7		11.8		11.3		12.2	
SNT	4.8		4.1		4.6		4.7		4.7		4.9		4.9	
EYE	4.4		3.6		4.4		3.6		4.7		4.2		4.4	
IOD	3.2		3.0		3.3		3.6		3.4		3.2		3.4	
TMP	2.1		2.1		2.2		2.3		1.9		2.1		2.3	
TEY	1.3		1.7		1.2		1.5		1.7		1.9		1.9	
TIB	15.8		14.5		15.4		14.9		15.7		15.8		15.9	
EN	2.8		2.3		2.7		2.5		2.6		2.3		2.8	
IN	3.0		2.3		2.6		2.7		3.0		2.6		2.7	
NS	2.1		1.8		1.8		2.0		1.9		1.9		2.0	
ML	8.1		7.6		8.3		7.6		8.1		8.3		8.7	
PL	14.1		12.9		14.0		13.7		14.8		14.6		15.1	
F1	2.8		2.3		2.7		2.5		3.0		3.2		3.3	
F2	3.0		3.3		3.2		3.3		3.4		3.6		3.5	
F3	4.9		5.1		5.5		4.9		5.1		6.0		6.1	
HDL/HDW	0.92		0.90		0.92		0.87		0.90		0.90		0.93	
HDL/SVL	0.34		0.30		0.32		0.31		0.33		0.31		0.32	
TIB/SVL	0.51		0.45		0.47		0.45		0.49		0.48		0.45	
TMP/SVL	0.07		0.06		0.07		0.07		0.06		0.06		0.06	
EYE/SNT	0.92		0.88		0.94		0.76		0.99		0.87		0.89	
Mean ± SD (F)			33 ± 1.2		10.4 ± 0.5		4.6 ± 0.3		4.1 ± 0.5		3.3 ± 0.2		2.2 ± 0.1	
Min-Max (F)			30.94–35.25		9.75–11.34		4.06–4.92		3.56–4.7		2.99–3.55		1.94–2.33	

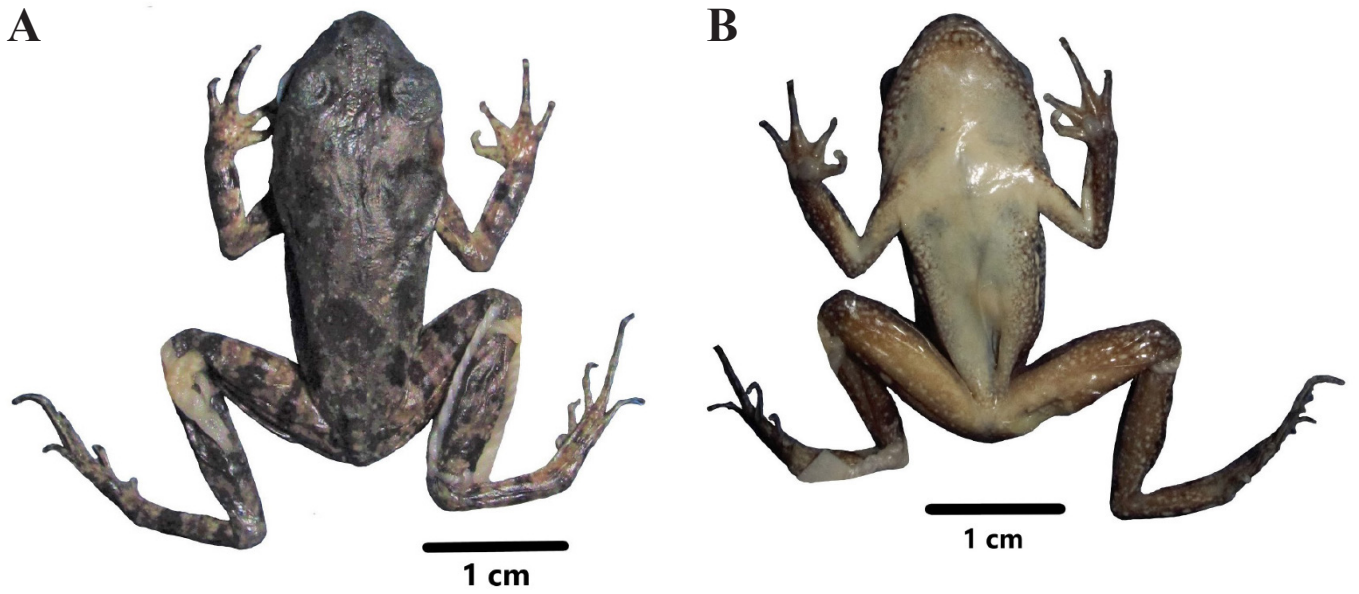


Fig. 4. Lateral view (A) and ventral view (B) of the holotype (VNUF A.2017.37) of *Leptobranchella namdongensis*, new species in preservative.

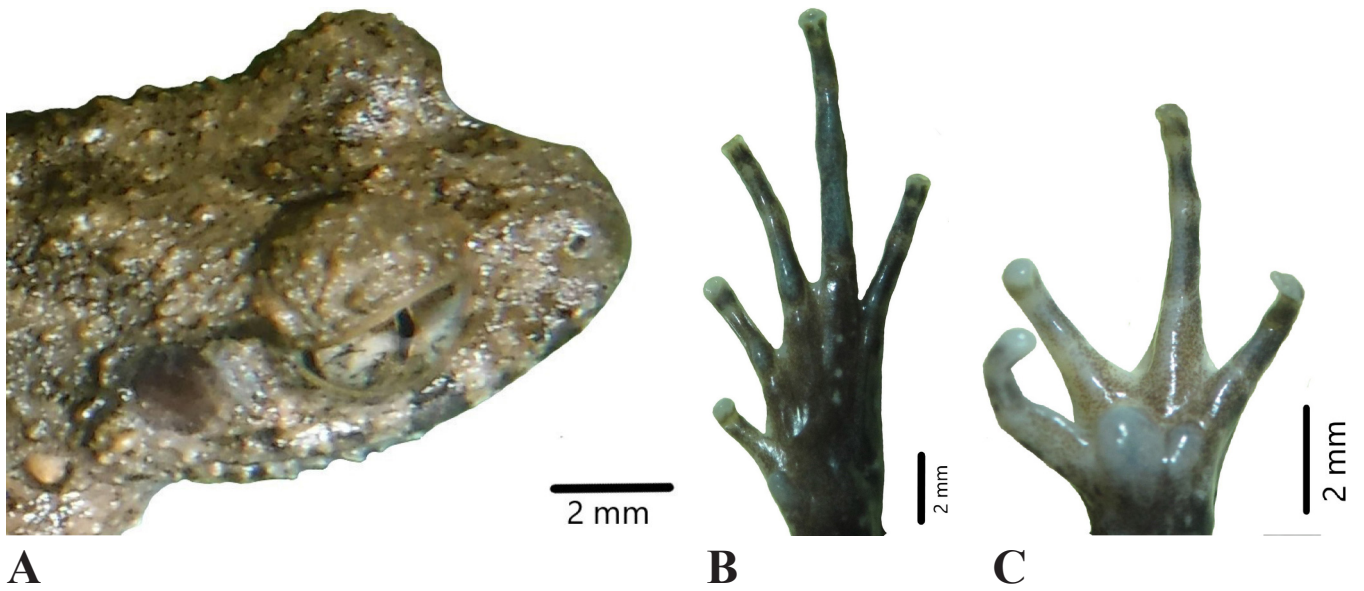


Fig. 5. Lateral view of the head (A), right foot (B) and right hand (C) of the holotype (VNUF A.2017.37) of *Leptobranchella namdongensis*, new species.

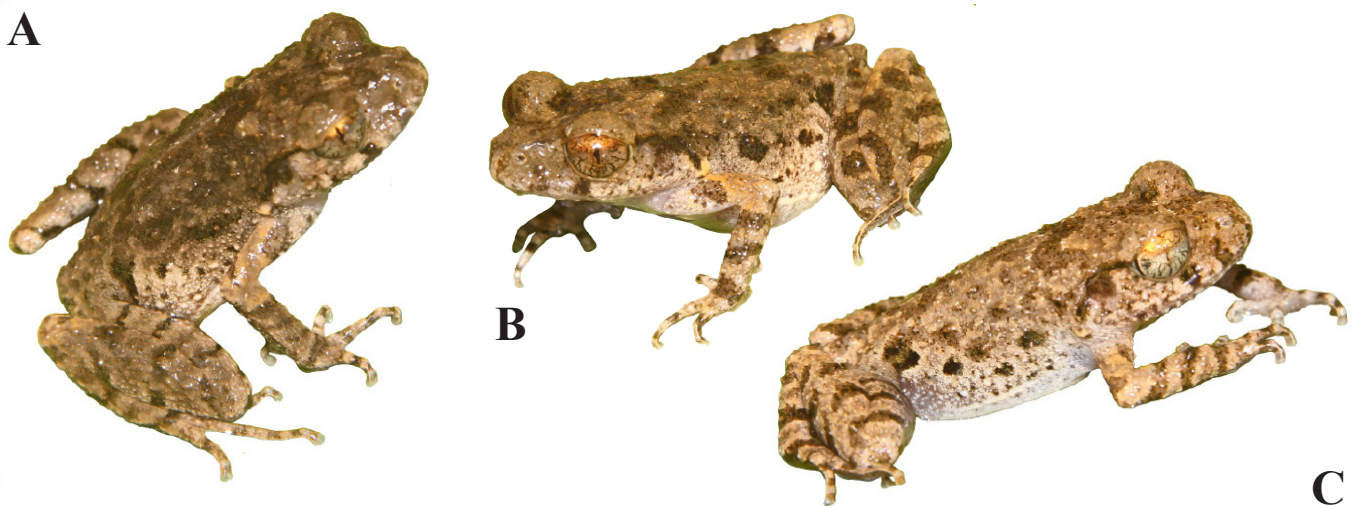


Fig. 6. Paratypes of *Leptobranchella namdongensis*, new species in life. A, female VNUF A.2017.95 (SVL 32.1mm); B, female VNMN2019.04 (SVL 33.0mm); C, female IEBR 4512 (SVL 32.2mm). Photos by Vinh Q. Luu.



Fig. 7. Habitat of *Leptobrachella namdongensis*, new species in Nam Dong Conservation Area, Thanh Hoa Province, Vietnam.

distinct black blotches; iris bicoloured, upper half copper, fading to golden in its lower half; head without dorsolateral markings.

**Description of holotype.** Habitus stocky. Size medium, head wider than long (HDL/HDW 0.92); snout obtusely pointed in dorsal view, slightly projecting beyond margin of lower jaw; nostril round, located closer to tip than to eye; canthus rostralis round; loreal region sloping; pupil vertical; eye diameter equal to snout length (EYE/SNT 0.92); tympanum distinct, round, tympanum diameter smaller than (48%) that of eye; tympanic rim not elevated relative to skin of temporal region; vomerine teeth absent; pineal ocellus absent; vocal sac openings present, located on either side of floor of mouth; tongue large, broad, with small notch at tip; supratympanic fold forming a distinct ridge, running from posterior corner of eye towards axillary gland; supratympanic ridge not smooth with few nodule (Fig. 5A). Forelimbs thin, slender; finger tips round, not broader than phalange width; relative finger lengths:  $I < II = IV < III$ ; nuptial pad absent; subarticular tubercles absent; a large, round inner palmar tubercle, distinctly separated from small, laterally compressed outer palmar tubercle; finger webbing absent and weak dermal fringes (Fig. 5C). Hindlimbs slender, tibia nearly half of snout-vent length (TIB/SVL 0.51). Tips of toes like those of fingers; relative toe lengths:  $I < II < V < III < IV$ ; subarticular tubercles absent, replaced by distinct dermal ridges; inner metatarsal tubercle small, oval, pronounced, outer metatarsal tubercle absent; webbing rudimentary between toes I–IV, absent between toes IV–V; toes with very weak lateral fringing (Fig. 5B). Skin texture in life; skin on entire dorsum with low, round tubercles, more dense in posterior part of the back; dorsal surface of thighs, upper arms and upper eyelid covered by small tubercles; ventral skin smooth; pectoral gland laterally compressed, 0.8 mm in diameter; femoral glands small, oval, approximately 1.1 mm in diameter, located on posteroventral surfaces of thighs, closer to knee than to vent; supra-axillary gland raised, 0.8 mm in diameter. Ventrolateral glands present, dorsolaterally compressed forming an incomplete line (Fig. 3).

**Colouration in life (Fig. 3).** Dorsum brown with grey markings, flanks and heels light-brown with some dark flecks; interorbital region with a dark bar; a W-shaped marking between axillae, an inverted V-shaped marking between sacrum; upper lip with dark brown bars; loreal and tympanic region with distinct dark brown markings, a dark brown stripe below supratympanic ridge, running from posterior corner of eye towards tympanum; dorsal surface of limbs with diffuse, transverse dark brown bars; fingers and toes with faint transverse bars; throat, chest and belly opaque white; outer edges of chin, thighs, arms and all of tibiotarsus brownish grey with small whitish spots; supra-axillary gland light-brown; femoral, pectoral and dorsolateral glands white; iris bicoloured, copper in upper half, fading to golden in its lower half.

**Colouration in preservative.** Dorsal surface grey; throat, chest and belly white; ventrolateral margins of throat and belly with brown speckling; ventral surface of thighs and arms cream to pale brown with white speckling; white macro glands and pectoral glands became indistinct in preservative (Fig. 4).

**Variation.** Measurements of the type series are shown in Table 3 and photographs of paratypes in life are shown in Fig. 6. Specimens vary in body size and colour pattern in life. Glands around cloacal opening vary in size and number. Tuberculation is more distinct in the male than in the females. In preservative dorsal skin texture varies from finely tuberculate (VNUF A.2017.37) to almost smooth (VNUF A.2017.95, VNMN2019.04, IEBR 4512, VNUF A.2018.15, VNMN2019.05, and IEBR 4513). Females are larger in body size (SVL 32.1–35.3;  $n=6$ ) compared to the male holotype (SVL 30.9;  $n=1$ ).

**Etymology.** Specific epithet is in reference to the type locality of the Nam Dong Conservation Area. We recommend “Nam Dong litter frog” as the common English name and “Cóc mảy nam động” as the Vietnamese name.

**Distribution and ecological notes.** *Leptobrachella namdongensis*, new species is currently known from Nam Dong Conservation Area and Pu Hu Nature Reserve (NR), Thanh Hoa Province, Vietnam. All specimens of the new species were found on rocks in small streams or near cascade streams in evergreen forest at elevations between 500 and 740 m a.s.l. (Fig. 7). *Leptobrachella namdongensis*, new species occurs sympatrically with *Leptobrachella ventripunctata*.

## DISCUSSION

The discovery of *Leptobrachella namdongensis* brings the total number of known species in the genus to 73 and the species number in Vietnam to 27 (Frost, 2019). It is likely that the number of species in the genus will continue to increase as a result of additional fieldwork and the combining of molecular and bioacoustic techniques to delineate species boundaries (Rowley et al., 2017a). Our genealogical analyses of the *Leptobrachella namdongensis*, new species corresponds well with previous phylogenetic studies (Rowley et al., 2017a).

Chen et al. (2018) assigned two specimens (IEBR\_ADPH049, IEBR\_ADPH101 with Genbank accession numbers MH055898, MH055899) collected from Pu Hu NR to a known species *Leptobrachella puhoatensis*. However, our data showed that these specimens are identical to *Leptobrachella namdongensis* with p-distance of 1%. Also, the Pu Hu NR (located in Thanh Hoa Province) is only 18 km is distance from Nam Dong Conservation Area and 68 km from Pu Hoat NR (located in Nghe An Province) to the south. Therefore, we have identified that two specimens (IEBR\_ADPH049, IEBR\_ADPH101 with GenBank accession numbers MH055898, MH055899) as being *Leptobrachella namdongensis*, new species, indicating the species is also distributed in Pu Hu NR, Thanh Hoa Province. Despite our best efforts, the two specimens (IEBR\_ADPH049 and IEBR\_ADPH101) could not be located and we could not refer to them in our study.

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