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Five new, microendemic Asian Leaf-litter Frogs (*Leptolalax*) from the southern Annamite mountains, Vietnam

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Abstract

The *Leptolalax applebyi* group of Asian leaf-litter frogs currently comprises four species of particularly small-bodied (<40 mm SVL) species distributed in the Central Highlands of Vietnam and northeastern Cambodia. In addition to their small size, the group is characterized by their morphological and genetic similarities, as well as their breeding habitat at headwaters of small mountain streams and seeps. A recent study suggested that at least two-thirds of the diversity of the group remained hidden within morphologically cryptic lineages. We expand upon the molecular, morphometric, and acoustic data and formally delineate and describe five of these lineages as distinct species: *Leptolalax ardens* **sp. nov**., *Leptolalax kalonensis* **sp. nov.**, *Leptolalax pallidus* **sp. nov.**, *Leptolalax maculosus* **sp. nov**., and *Leptolalax tadungensis* **sp. nov.** Due to habitat loss, the current ranges of these species are likely to be a fraction of their historical extent and under continued threat from deforestation.

Key words: Bioacoustics, *Leptolalax ardens* **sp. nov**., *Leptolalax kalonensis* **sp. nov.**, *Leptolalax pallidus* **sp. nov.**, *Leptolalax maculosus* **sp. nov**., *and Leptolalax tadungensis* **sp. nov.**, microendemism, Southeast Asia

Introduction

The genus *Leptolalax* Dubois 1983 is a group of forest-dependent frogs, currently known to comprise 44 species (Frost 2015). Frogs in the genus inhabit the forest floor and rocky streams in hilly evergreen forest throughout Southeast Asia, southern China and northeastern India (Frost 2015). *Leptolalax* are characteristically dull brown and small (<60 mm SVL), and often difficult to detect in the field and subsequently identify. As a result of both increased survey effort in the region and the addition of acoustic and molecular data in delineating species boundaries in the genus, over half of all *Leptolalax* species have been described since 2000 (Frost 2015).

The *Leptolalax applebyi* species group (*sensu* Rowley *et al*. 2015) comprises four species of particularly small (<40 mm SVL) *Leptolalax* species distributed in the Central Highlands of Vietnam and northeastern Cambodia; *L. applebyi* Rowley & Cao 2009, *L. bidoupensis* Rowley *et al*. 2011, *L. melicus* Rowley *et al*. 2010, and *L. pyrrhops* Poyarkov *et al*. 2015. In addition to their small size, the group is characterized by their morphological similarity (with most having a brown dorsum, dark brownish red ventral surface with white speckling and black markings on the flanks), molecular similarity (forming a monophyletic group within the genus), quiet rasping advertisement calls, and breeding habitat at headwaters of small mountain streams and seeps (Rowley *et al*. 2015).

A recent study provided evidence of a significant species richness underestimation in the *Leptolalax applebyi* group, suggesting that at least two-thirds of the diversity of the group remained hidden within morphologically

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cryptic lineages (Rowley *et al*. 2015). Here we expand upon the molecular, morphometric, and acoustic data and formally delineate and describe five of the lineages identified in that study as distinct species. Additional evidence (eg. additional specimens or acoustic data) is required in order to delineate the sixth lineage ('Lineage 7') identified in Rowley *et al*. (2015).

Material and methods

Surveys: *Leptolalax* specimens were collected between 2006 and 2011 from 22 sites (defined as localities >1 km apart) in the Central Highlands of Vietnam and adjoining northeastern Cambodia (Fig. 1). Sites are all within broadleaf evergreen forest between 200–1935 m asl. Most frogs were encountered during nocturnal surveys at breeding sites, where the advertisement calls of males increased detectability. Geographic coordinates were obtained using a Garmin GPSMAP 60CSx GPS receiver and recorded in datum WGS 84.

FIGURE 1. Map showing the localities where specimens in the *Leptolalax applebyi* group were collected in Cambodia and Vietnam. Colours of localities assigned based on molecular lineages. Paler areas are higher elevation. Dark grey lines show country boundaries, pale grey lines show watershed boundaries and blue lines show rivers.

A total of 87 adult male and 19 adult female specimens belonging to the *L. applebyi* group were collected. Prior to preservation, tissues (liver or thigh muscle) was removed for molecular analysis and stored in EDTA/DMSO or 80% ethanol. Specimens were then fixed in 10% formalin and then stored in 70% ethanol or fixed and stored in 80% ethanol. Specimens were deposited at the American Museum of Natural History (AMNH) in New

York, USA, Australian Museum (AMS) in Sydney, Australia, Institute of Ecology and Biological Resources (IEBR) in Hanoi, Vietnam, Museum of Vertebrate Zoology, University of California Berkeley (MVZ) in Berkeley, USA, North Carolina Museum of Natural Sciences (NCSM) in Raleigh USA, University of Science, Ho Chi Minh City (UNS) in Ho Chi Minh City, Vietnam, Vietnam National Museum of Nature (VNMN) in Hanoi, Vietnam and Zoologisches Forschungsmuseum Alexander Koenig (ZMFK) in Bonn, Germany (Appendix I).

Molecular data: Genomic DNA was extracted from EDTA/DMSO or ethanol preserved tissues using DNeasy Blood and tissue kit (QIAGEN GmbH, Hilden, Germany), using the protocols for purification of total DNA from animal tissues. We amplified a ~550 bp section of 16S (mtDNA) using the primers (5'-3') 16AR CGCCTGTTTATCAAAAACAT and 16AB CCGGTCTGAACTCAGATCACGT (Palumbi 1991). PCR amplification was carried out in 25ul reactions with 1000 ng of genomic DNA, 1 x Reaction Buffer (Bioline My Taq Red Reagent Buffer), 2 pmol corresponding primers and Bioline My Taq Red DNA polymerase (0.5 unit). Negative controls were included in each PCR. Thermocycling was performed on an Eppendorf Mastercycler EpS (Eppendorf, Hamburg, Germany) under the following conditions: initial denaturation 94°C (2 mins), 2 cycles of 94°C (20s) denaturation, 52°C (40s) annealing and 72°C (60s) extension, followed by 33 cycles of 94°C (20s) denaturation, 50°C (40s) annealing and 72°C (50s) extension, followed by a final extension step at 72°C for 5 mins. All PCR products were purified using Exo-Sap-IT (USB Corporation, OH, USA), and directly sequenced at the Australian Genome Research Facility, Sydney and Macrogen (Seoul, Korea). Sequences were edited with reference to chromatograms using Sequencher v. 4.10 (Gene Codes, Ann Arbor, MI).

In addition to the newly collected specimens, all species belonging to the genus *Leptolalax* for which homologous sequences were available on GenBank (27 of the 44 known species) were included in the alignment used for phylogenetic analysis. *Leptobrachium* cf. *chapaense* was included in the analysis as an outgroup. Locality information and accession numbers for all sequences included in the analysis can be found in Table 1.

Phylogenetic analyses: The data set was aligned using the ClustalW algorithm as implemented in MEGA 5 (Tamura *et al*. 2011) using the default parameters. We followed the methods of Rowley *et al*. 2015 and retained indels, however removing indels resulted in trees with a near-identical topology. We used Akaike Information Criterion as implemented in jModelTest 2.1.4 (Darriba *et al*. 2012) to select the best-fit model of nucleotide substitution, which was then used in model-based phylogenetic inference.

Maximum-likelihood phylogenetic analyses were performed in GARLI 2.0 (Zwickl 2006) under a GTR+I +Γ model of evolution (General Time Reversible model with Gamma distributed substitution rates and a proportion of the sites invariable; model parameters estimated during the search). 100 independent searches were performed, each starting with a random tree. Each search was terminated after 200,000 generations with no significant improvement in likelihood. The best likelihood from these runs was selected as our maximum-likelihood estimate, and statistical support for this topology was obtained by running 1,000 bootstrap replicates in GARLI with the same settings, except that the termination criterion was reduced to 10,000 generations with no significant topological improvement. Support values were plotted on the optimal Maximum Likelihood topology using SumTrees 3.3.1 (Sukamaran & Holder 2010). We consider branches receiving ≥70% bootstrap support to be well-supported following the suggestion of Hillis & Bull (1993).

Bayesian phylogenetic analyses were performed in MrBayes 3.2 (Ronquist *et al*. 2012) also under a GTR+I +Γ model. Four independent Markov Chain Monte Carlo searches were run for 2 million generations, sampled every 2000 generations, each with four chains, and default settings for most priors. Output files were examined visually in Tracer v1.5 (Rambaut & Drummond 2007), to assess stationarity and determine the number of generations to remove as burn-in. We considered 200,000 generations from each run as burn-in, and thus removed 100 trees before summarizing topology and posterior probabilities. Trees were visualized using FigTree v1.3.1 (Rambaut & Drummong 2009). We consider branches receiving ≥0.95 posterior probabilities to be well-supported, following the suggestion by Wilcox *et al.* (2002).

We also calculated uncorrected pairwise sequence divergence (pairwise deletion) using MEGA 5.

Morphological data and analyses: Morphometric data were taken for all described species in the *Leptolalax applebyi* group and "Lineages" 3, 5, 6, 8 and 9 identified in Rowley *et al*. (2015). We did not include measurements from "Lineage 7" identified in Rowley *et al*. (2015) as we lacked acoustic data for the lineage and could not morphologically delineate the lineage from all other lineages based upon our limited sample size of six adult males and a subadult female (Rowley *et al*. 2015). Measurements were taken to the nearest 0.1 mm with digital callipers and include snout–vent length (SVL); head length from tip of snout to rear of jaws (HDL); head width at the

TABLE 1. List of voucher specimens and GenBank accession numbers for all DNA sequences included in the analysis.

Species	Locality	Voucher #	16S	Source
Leptolalax aereus	Vietnam, Quang Binh Province	RH60165	JN848437	Rowley *et al.* 2010a
Leptolalax applebyi	Quang Nam Province, Vietnam	AMS R 171703	HM133597	Rowley *et al.* 2010b
Leptolalax applebyi	Kon Tum Province, Vietnam	AMS R 173778	KR018108	Rowley *et al.* 2015
Leptolalax applebyi	Kon Tum Province, Vietnam	AMS R 173737	KU530188	This study
Leptolalax applebyi	Kon Tum Province, Vietnam	AMS R 173635	KU530189	This study
Leptolalax arayai	Malaysia, Borneo	BORNEENSIS 22931	AB847558	Matsui *et al.* 2014a
Leptolalax ardens **sp. nov**. (Lineage 3)	Gia Lai Province, Vietnam	VNMN 04707/AMS R 176454	KR018109	Rowley *et al.* 2015
Leptolalax ardens **sp. nov**. (Lineage 3)	Gia Lai Province, Vietnam	AMS R 176463	KR018110	Rowley *et al.* 2015
Leptolalax ardens **sp. nov**. (Lineage 3)	Gia Lai Province, Vietnam	AMS R 176467	KR018111	Rowley *et al.* 2015
Leptolalax bidoupensis	Lam Dong Province, Vietnam	NAP-0145	KP017573	Poyarkov *et al.* 2015
Leptolalax bidoupensis	Lam Dong Province, Vietnam	NAP-01458	KP017574	Poyarkov *et al.* 2015
Leptolalax bidoupensis	Lam Dong Province, Vietnam	AMS R 173133	HQ902880	Rowley *et al.* 2011
Leptolalax bidoupensis	Lam Dong Province, Vietnam	NCSM 77321	HQ902883	Rowley *et al.* 2011
Leptolalax bidoupensis	Lam Dong Province, Vietnam	AMS R 173134	HQ90288	Rowley *et al.* 2011
Leptolalax bidoupensis	Lam Dong Province, Vietnam	NCSM 77320	HQ902882	Rowley *et al.* 2011
Leptolalax bourreti	Lao Cai Province, Vietnam	AMS R 177673	KR018124	Rowley *et al.* 2015
Leptolalax dringi	Malaysia, Borneo	KUHE:55610	AB847553	Matsui *et al.* 2014a
Leptolalax eos	Laos, Phongsaly Province	MNHN:2004.0278	JN848450	Ohler *et al*. 2011
Leptolalax firthi	Kon Tum Province, Vietnam	AMS R 176524	JQ739206	Rowley *et al*. 2012
Leptolalax fritinniens	Malaysia, Borneo	KUHE 55371	AB847557	Matsui *et al.* 2014a
Leptolalax gracilus	Malaysia, Borneo	KUHE 55624	AB847560	Matsui *et al.* 2014a
Leptolalax hamidi	Malaysia, Borneo	KUHE 17545	AB969286	Matsui *et al.* 2014b
Leptolalax heteropus	Malaysia, Peninsula	KUHE 15487	AB530453	Matsui *et al.* 2014a
Leptolalax isos	Gia Lai Province, Vietnam	VNMN A 2015.4/AMS R 176480	KT824769	Rowley *et al*. 2014
Leptolalax kalonensis **sp. nov.** (Lineage 6)	Binh Thuan Province, Vietnam	IEBR A.2014.15	KR018114	Rowley *et al*. 2015
Leptolalax kalonensis **sp. nov.** (Lineage 6)	Binh Thuan Province, Vietnam	AMNH A191762	KR018115	Rowley *et al*. 2015
Leptolalax kalonensis **sp. nov.** (Lineage 6)	Binh Thuan Province, Vietnam	IEBR A.2014.16	KR018116	Rowley *et al*. 2015

……*continued on the next page*

TABLE 1. (Continued)

Species	Locality	Voucher #	16S	Source
Leptolalax kalonensis **sp. nov.** (Lineage 6)	Binh Thuan Province, Vietnam	AMNH A191765	KR018117	Rowley *et al*. 2015
Leptolalax laui	China, Shenzhen	SYS A002057	KM014546	Sung *et al*. 2014
Leptolalax liui	China, Jiangxi Province	SYS A001620	KM014549	Sung *et al*. 2014
Leptolalax maculosus **sp. nov.** (Lineage 8)	Ninh Thuận Province, Vietnam	AMS R 177660	KR018119	Rowley *et al*. 2015
Leptolalax maculosus **sp. nov.** (Lineage 8)	Ninh Thuận Province, Vietnam	ZFMK 96600	KR018120	Rowley *et al*. 2015
Leptolalax marmoratus	Malaysia, Borneo	KUHE 53227	AB969289	Matsui *et al.* 2014b
Leptolalax maurus	Malaysia, Borneo	SP 21450	AB847559	Matsui *et al.* 2014a
Leptolalax melicus	Ratanakiri Province, Cambodia	MVZ 258197	HM133599	Rowley *et al*. 2010
Leptolalax melicus	Ratanakiri Province, Cambodia	MVZ 258198	HM133600	Rowley *et al*. 2010
Leptolalax melicus	Ratanakiri Province, Cambodia	MVZ 258199	HM133601	Rowley *et al*. 2010
Leptolalax minimus	Thailand, Chiangmai Province	-	JN848369	Ohler *et al*. 2011
Leptolalax nyx	Vietnam, Ha Giang Province	AMNH A163810	DQ283381	Frost *et al*. 2006
Leptolalax oshanensis	China, Sichuan Province	SYS A001830	KM014810	Sung *et al*. 2014
Leptolalax pallidus **sp. nov** (Lineage 5)	Lam Dong Province, Vietnam	UNS00510	KR018112	Rowley *et al.* 2015
Leptolalax pallidus **sp. nov** (Lineage 5)	Lam Dong Province, Vietnam	UNS00512	KR018113	Rowley *et al.* 2015
Leptolalax pallidus **sp. nov** (Lineage 5)	Lam Dong Province, Vietnam	UNS00511	KU530190	This study
Leptolalax pictus	Malaysia, Borneo	UNIMAS 8705	KJ831295	Oberhummer *et al*. 2014
Leptolalax pluvialis	Vietnam, Lao Cai Province	MNHN:1999.5675	JN848391	Ohler *et al*. 2011
Leptolalax pyrrhops	Lam Dong Province, Vietnam	ZMMU A-5208	KP017575	Poyarkov *et al*. 2015
Leptolalax pyrrhops	Lam Dong Province, Vietnam	ZMMU A-4873 (ABV-00213)	KP017576	Poyarkov *et al*. 2015
Leptolalax pyrrhops	Lam Dong Province, Vietnam	VNMN A2015.02	KP017577	Poyarkov *et al*. 2015
Leptolalax pyrrhops	Lam Dong Province, Vietnam	ZMMU A-4873 (ABV-00215)	KP017578	Poyarkov *et al*. 2015
Leptolalax sabahmontanus	Malaysia, Borneo	BORNEENSIS 12632	AB847551	Matsui *et al.* 2014a
Leptolalax sp. (Lineage 7)	Dak Lak Province, Vietnam	AMS R 177663	KR018118	Rowley *et al*. 2015
Leptolalax tadungensis **sp.nov.** (Lineage 9)	Dak Nong Province, Vietnam	UNS00515	KR018121	Rowley *et al*. 2015
Leptolalax tadungensis **sp.nov.** (Lineage 9)	Dak Nong Province, Vietnam	UNS00517	KR018122	Rowley *et al*. 2015
Leptolalax ventripunctatus	Laos, Phongsaly Province	MNHN 2005.0116	JN848410	Ohler *et al*. 2011
Leptolalax zhangyapingi	Thailand: Chiang Mai	KJ-2013	JX069979	Jiang *et al*. 2013
Leptobrachium cf. *chapaense*	Vietnam, Lao Cai Province	AMS R 171623	KR018126	Rowley *et al*. 2015

commissure of the jaws (HDW); snout length from tip of snout to the anterior corner of eye (SNT); diameter of the exposed portion of the eyeball (EYE); interorbital distance (IOD); horizontal diameter of tympanum (TMP); distance from anterior edge of tympanum to posterior corner of the eye (TEY); and tibia length with the hindlimb flexed (TIB), manus length from tip of third digit to base of inner palmar tubercle (ML), pes length from tip of fourth toe to base of the inner metatarsal tubercle (PL), maximum diameter of pectoral gland (PEC), maximum diameter of femoral gland (FEM), and maximum diameter of humeral gland (HUM). Sex was determined by direct observation of calling in life, the presence of internal vocal sac openings (vocal slits) and/or gonadal inspection. Mass was recorded in life (to the nearest 0.1 g) for *L. applebyi, L. bidoupensis* and "Lineage 3" (Rowley *et al*. 2015) using Pesola scales.

In order to determine morphometric differences among molecular lineages, we performed Principal Component Analyses (PCA) using varimax rotation based on morphometric values for males in the *Leptolalax applebyi* group, excluding "Lineage 7" (Rowley *et. al*. 2015), and including the recently described *L. pyrrhops*. We did not analyse female morphometrics due to the low sample size (n=19 adult females) and absence of female specimens for one of the lineages. All specimens were measured by a single author (JR), except for *L. pyrrhops,* for which measurements were taken from Poyarkov *et al*. (2015). Due to the poor preservation of several specimens, we removed ML and PL from the analysis. As in Rowley *et al*. (2015), we then examined each variable that contributed highly to the factor loadings (>0.80). As our measurements were non-normal, we performed nonparametric Wilcoxon/Kruskal-Wallis tests and Nonparametric Comparisons on these variables for each molecular lineage or species pair using the Wilcoxon Method. For variables other than SVL, we removed the effect of SVL by using ratios of the variable relative to SVL in these tests. We did not use Bonferroni adjustments for multiple comparisons because these adjustments have a number of mathematical and logical flaws, and because they may inflate Type II error in situations with low statistical power (Perneger 1998, Moran 2003, Nakagawa 2004). In addition, we were interested in elucidating morphometric differences between each lineage and all other lineages rather than in a general null hypothesis that none of the species were morphometrically different. Statistical analyses were performed on male measurements only using JMP software (ver. 10.0.2; SAS Institute Inc. Cary, NC, USA). In addition to morphometric differences, we used several discrete morphological characteristics to aid in diagnosing species: skin texture (TEX; smooth or with only low tubercles versus distinctly tuberculate), supratympanic line coloration (STF; distinctly black versus less distinct and brownish) and iris colouration in life (IRI; distinctly bicoloured versus relatively uniformly golden or bronze) to differentiate species.

For *Leptolalax* species from mainland Southeast Asia outside the *L. applebyi* group, we obtained comparative morphological data from museum specimens and photographs of these specimens in life (Appendix I) as well as from the literature: *L. aereus* (Rowley *et al*. 2010b), *L. botsfordi* (Rowley *et al*. 2013), *L. bourreti* (Dubois 1983; Ohler *et al*. 2011), *L. croceus* (Rowley *et al.* 2010c), *L. eos* (Ohler *et al*. 2011), *L. firthi* (Rowley *et al*. 2012), *L. fuliginosus* (Matsui 2006), *L. heteropus* (Boulenger 1900), *L. isos* (Rowley *et al*. 2015), *L. kecil* (Matsui *et al*. 2009), *L. melanoleucus* (Matsui 2006), *L. minimus* (Ohler *et al*. 2011), *L. nahangensis* (Lathrop *et al*. 1998), *L. nyx* (Ohler *et al*. 2011), *L. pelodytoides* (Boulenger 1893, 1908; Ohler *et al*. 2011), *L. platycephalus* (Dehling 2012), *L. pluvialis* (Ohler *et al.* 2000, 2011), *L. solus* (Matsui 2006), *L. sungi* (Lathrop *et al.* 1998), *L. tuberosus* (Inger *et al.*1999; Rowley *et al*. 2010c), *L. ventripunctatus* (Fei *et al*. 1991, 2009, 2010), *L. zhangyangpingi* (Jiang *et al*. 2013). Due to the degree of undiagnosed diversity within the genus, where available, we relied on examination of type specimens, topotypic material and/or original species descriptions.

Acoustic data: Methods for recording and analysing advertisement calls followed that of Rowley *et al*. (2015). We analysed call recordings from 25 individuals representing all molecular lineages in the *Leptolalax applebyi* group except for "Lineage 7" in Rowley *et al*. (2015), for which no recordings are available (Table 2). We also analysed measurements taken from Poyarkov *et al*. (2015) of the advertisement call of a single *L. pyrrhops*. In recording advertisement calls, we used an Edirol R–09 WAVE/MP3 Recorder (44.1 kHz sampling rate and 24–bit encoding) with a Røde NTG–2 condenser shotgun microphone or Zoom H4n handy Mobile 4-Track recorder (44.1 kHz sampling rate and 24–bit encoding). Calls were recorded at a distance of approximately 0.1–0.3 m and ambient temperatures were taken immediately after recordings using a Kestrel 3500 or 4000 hand–held weather meter. Calls were analysed with Raven Pro 1.3© software (http://www.birds.cornell.edu/raven). Audiospectrograms in figures were calculated with fast–Fourier transform (FFT) of 1024 points, 50% overlap and 172 Hz grid–spacing, using Hanning windows. In analysing and describing advertisement calls, we used the terminology of Duellman (1970), except that we defined a single call as vocalisations produced during a single expiration. Temporal and spectral

parameters of calls were measured using the definitions of Cocroft & Ryan (1995), except for fundamental frequency, where the definition of Duellman (1970) was used. For each call recording, we measured the call duration (ms), intercall interval (ms), number of notes per call, internote interval (ms), percent of call composed of note 1, number of pulses per note and dominant frequency (Hz). Comparative advertisement call characters for *Leptolalax* species were taken from references, with advertisement calls known for 11 of the 22 species of *Leptolalax* known from mainland Southeast Asia (Matsui 1997, 2006; Jiang *et al*. 2002; Malkmus *et al*. 2002; Matsui *et al*. 2009, 2014a, 2014b; Xu *et al*. 2005; Rowley & Cao 2009; Rowley *et al.* 2010a, 2010b, 2010c, 2011, 2012, 2013, 2015; Sukumaran *et al.* 2010; Dehling & Matsui 2013; Poyarkov *et al*. 2015). To maintain consistency and facilitate meaningful comparisons, we have used the terminology defined above to compare calls, regardless of terms used in these references.

TABLE 2. List of advertisement calls analysed and associated voucher specimens. Lineages (in parentheses) refer to molecular lineages identified in Rowley *et al*. 2015.

Species	Specimen
Leptolalax applebyi	AMS R 173635
Leptolalax applebyi	AMS R 171703
Leptolalax applebyi	No voucher
Leptolalax bidoupensis	AMS R 173133
Leptolalax bidoupensis	AMS R 173135/UNS 00101
Leptolalax bidoupensis	No voucher
Leptolalax melicus	MVZ 258198
Leptolalax melicus	MVZ 258199
Leptolalax ardens **sp. nov.** (Lineage 3)	No voucher
Leptolalax ardens **sp. nov.** (Lineage 3)	VNMN 04712/AMS R 176459
Leptolalax ardens **sp. nov.** (Lineage 3)	UNS 00534/AMS R 176466
Leptolalax ardens **sp. nov.** (Lineage 3)	No voucher
Leptolalax ardens **sp. nov.** (Lineage 3)	No voucher
Leptolalax ardens **sp. nov.** (Lineage 3)	AMS R 176467
Leptolalax ardens **sp. nov.** (Lineage 3)	No voucher
Leptolalax pallidus **sp. nov**. (Lineage 5)	ZFMK 96598
Leptolalax pallidus **sp. nov**. (Lineage 5)	ZFMK 96599
Leptolalax pallidus **sp. nov**. (Lineage 5)	UNS00510
Leptolalax kalonensis **sp. nov.** (Lineage 6)	AMNH A191770
Leptolalax maculosus **sp. nov.** (Lineage 8)	UNS00513
Leptolalax maculosus **sp. nov.** (Lineage 8)	AMS R 177660
Leptolalax tadungensis **sp. nov.** (Lineage 9)	UNS 00526
Leptolalax tadungensis **sp. nov.** (Lineage 9)	UNS00516
Leptolalax tadungensis **sp. nov.** (Lineage 9)	AMS R 177666
Leptolalax tadungensis **sp. nov.** (Lineage 9)	UNS 00527

Results

Molecular data. Phylogenetic relationships revealed using 16S sequences from 32 individuals of the *L. applebyi* group largely correspond to those recovered by Rowley *et al*. (2015) using fewer samples but additional genes (16S, Cytochrome *b*, NTF3, NCX, and SLC8A3; Fig. 2). The six lineages identified by Rowley *et al*. (2015) as likely to represent unnamed species (Lineages 3, 5, 6, 7, 8 and 9) were also recovered in our phylogenetic sampling. The recently described *L. pyrrhops* grouped with other southern species in the *L. applebyi* group (Clade

B1 of Poyarkov *et al.* 2015). Uncorrected sequence divergence among all lineages or species in the *L. applebyi* group was 4.5–7.5% at the 16S gene fragment analysed. Variation within species in the group was 0.0–0.6%.

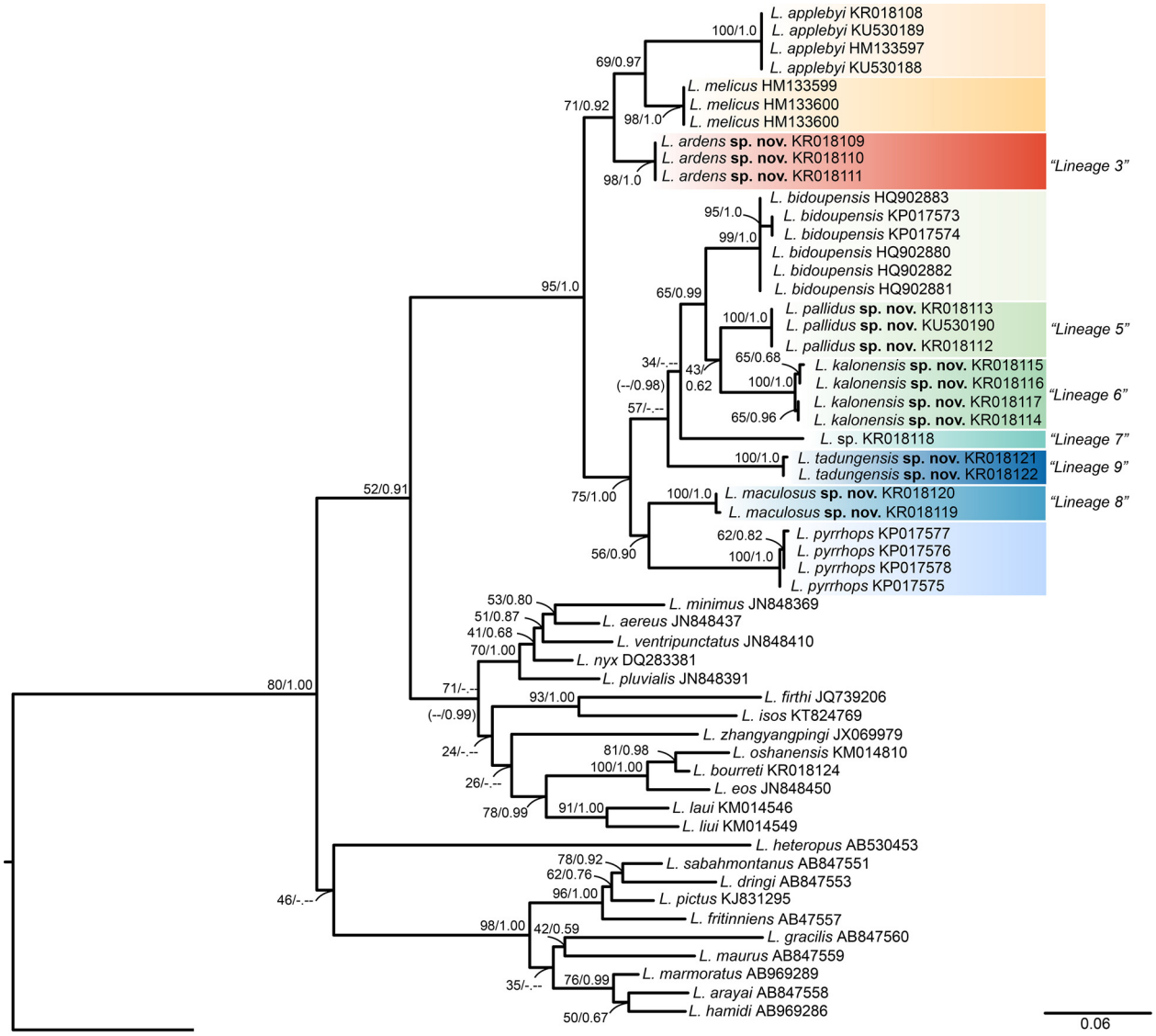

FIGURE 2. Maximum-likelihood (ML) tree based on 16S ribosomal RNA mitochondrial gene sequences for the *Leptolalax applebyi* group (colored region) and outgroups. Bayesian inference (BI) produced near-identical topology. Numbers on branches are ML bootstrap values and Bayesian posterior probabilities. Lineages 3, 5, 6–9 correspond to those identified in Rowley *et al*. (2015).

FIGURE 3. Three of the four previously described species in the *Leptolalax applebyi* group (A) *Leptolalax applebyi* (Kon Tum Province, Vietnam), (B) *L. bidoupensis* (Lam Dong Province, Vietnam), (C) *L. melicus* (Ratanakiri Province, Cambodia).

Morphological data. Frogs were morphologically similar, all with a brown dorsum, dark lateral blotches and a dark-coloured (either black or darker brown and less distinct) supratympanic fold (Fig. 3). Adult males ranged from 18.5–34.3 mm SVL and females from 21.7–33.9 mm. Principal component analyses (PCA) of male morphometrics revealed that the majority of the variance (67.9%) was explained by the first factor, PC1 (Eigen value = 8.15). This factor had high loadings for SVL, HDW, SNT, EYE, IOD, TMP, TEY and TIB, suggesting that PC1 is strongly influenced by body size. PC2, which had moderate factor loadings for PEC, FEM and HUM, explained 10.2% of the variance (Eigen value = 1.22). See Table 3 for PCA factor loadings.

TABLE 3. Rotated factor loadings of a Principal Component Analysis of morphometric comparisons among males of the *Leptolalax applebyi* group.

	PC1	**PC2**
SVL	**0.96681**	-0.10605
HDL	0.74829	-0.00537
HDW	**0.96195**	-0.08743
SNT	**0.87998**	-0.19694
EYE	**0.93381**	-0.07183
IOD	**0.86993**	-0.21852
TMP	**0.84809**	-0.28919
TEY	**0.84412**	-0.06931
TIB	**0.95399**	-0.08094
PEC	0.59402	0.58085
FEM	0.53291	0.58524
HUM	0.59281	0.58230

In order to translate these data into more diagnostically relevant information, we performed univariate analyses of those variables that were identified as most relevant by PCA (SVL, HDW, SNT, EYE, IOD, TMP, TEY and TIB), along with PEC, given its use in delineating species in the group (eg. Rowley *et al.* 2010b, Rowley *et al*. 2012). SVL (Wilcox, $Chi^2 = 72.3$, $p < 0.001$), HDW/SVL (Wilcox, $Chi^2 = 19.0$, $p = 0.015$), EYE/SVL (Wilcox, $Chi^2 = 33.5$, $p < 0.001$), TMP/SVL (Wilcox, $Chi^2 = 16.9$, $p = 0.307$), TEY/SVL (Wilcox, $Chi^2 = 27.7$, $p = 0.001$), TIB/SVL (Wilcox, $Chi^2 = 42.8$, $p < 0.001$), and PEC/SVL (Wilcox, $Chi^2 = 21.6$, $p = 0.003$) varied significantly among lineages. The most obvious difference between lineages was body size (Figure 4A), with non-overlapping SVL ranges among males of many species (Table 4). In addition to morphometric data, we also analysed a series of discrete characters. By categorizing major differences in skin texture, supratympanic line coloration and iris coloration, we were able to further differentiate most species on the basis of morphology. These morphological features are explained in Tables 4–6 and in the "comparison" sections below.

Acoustic data. Analysis of calls was complicated by the relatively low number of individuals recorded, uneven sample size per lineage and the correlation of spectral and temporal call parameters to body size and air temperature (which ranged from 12.9–26.4°C). Mean dominant frequency (kHz) was usually correlated with SVL (mm), and mean internote interval (ms), mean note repetition rate (notes/s) and mean relative duration of note 1 (%) were correlated with temperature (Rowley *et al*. 2015). Despite these limitations, call structure varied considerably, with the advertisement calls of the lineages differing in terms of number of notes, the presence, duration and number of pulses in an introductory note, pulse number in non-introductory notes and note repetition rate (Table 7; Figures 5–6). Therefore, advertisement calls were important in diagnosing most of the new taxa.

Conclusion. Based upon our examination of morphological and acoustic data, as well as additional molecular sampling, we conclude that the five molecular lineages examined represent distinct species. Frogs in each lineage differed by >4.5% uncorrected sequence divergence at the 16S gene fragment examined, varied in at least one morphological character and had unique male advertisement calls. Diagnosable by molecular, morphological and acoustic characters, we describe the five new species below.

TABLE 4. Summary of comparisons among males of species in the *Leptolalax applebyi* group, showing only morphometric characters that differed significantly among species pairs using nonparametric Wilcoxon/Kruskal-Wallis tests. Measurements marked with an asterisk (*) represent non-overlapping measurements for males. See methods for abbreviations.

	L. applebyi	*L. bidoupensis*	*L. melicus*	*L. pyrrhops*	*L. ardens* **sp. nov.** (Lineage 3)	*L. pallidus* **sp. nov.** (Lineage 5)	*L. kalonensis* **sp. nov.** (Lineage 6)	*L. maculosus* **sp. nov.** (Lineage 8)	*L. tadungensis* **sp. nov.** (Lineage 9)
L. applebyi									
L. bidoupensis	SVL, HDW, PEC, IRI								
L. melicus	EYE, PEC	SVL, TIB, TEY, IRI							
L. pyrrhops	SVL*, TIB, TEY, EYE	SVL*, TIB, EYE, IRI	SVL*, TIB, TEY, EYE						
L. ardens **sp. nov.** (Lineage 3)	SVL, TIB, HDW, EYE, PEC	SVL, TIB, EYE, IRI	SVL, TEY	SVL*, TMP, TEY, EYE					
L. pallidus **sp. nov.** (Lineage 5)	SVL*, TIB, HDW, EYE, PEC, STF, TEX	SVL, TIB, TMP, IRI, STF, TEX	SVL*, TEY, STF, TEX	SVL*, EYE, STF, TEX	SVL, TMP, STF, TEX				
L. kalonensis **sp. nov.** (Lineage 6)	SVL*, TIB, EYE, PEC	SVL*, TIB, EYE, IRI	SVL*, TEY	SVL*, TMP, TEY, EYE	SVL*	SVL, TMP, STF, TEX			
L. maculosus **sp. nov.** (Lineage 8)	SVL*, HDW*, EYE, PEC	TIB, IRI	SVL*, TEY	SVL*, TEY, EYE	SVL	STF, TEX	SVL		
L. tadungensis **sp. nov.** (Lineage 9)	SVL*, EYE, PEC	HDW, TEY, IRI	SVL*, TIB	SVL*, TIB, TEY, EYE	SVL, TIB	TIB, TEY, STF, TEX	SVL, TIB	TIB	

TABLE 5. Measurements (mm) of male *Leptolalax applebyi* species group. Abbreviations defined in text.

	L. applebyi	*L. bidoupensis*	*L. melicus*	*L. pyrrhops*	*L. ardens* **sp. nov.** (Lineage 3)	*L. pallidus* **sp. nov.** (Lineage 5)	*L. kalonensis* **sp. nov.** (Lineage 6)	*L. maculosus* **sp. nov.** (Lineage 8)	*L. tadungensis* **sp. nov.** (Lineage 9)
SEX	Male (n=9)	Male (n=12)	Male (n=8)	Male (n=7)	Male (n=16)	Male (n=8)	Male (n=16)	Male (n=3)	Male (n=10)
SVL	20.8 (19.6–22.3)	23.6 (18.5–25.4)	20.7 (19.5–22.7)	33.2 (30.8–34.3)	22.8 (21.3–24.7)	25.6 (24.5–27.7)	27.4 (25.8–30.6)	25.5 (24.2–26.6)	25.0 (23.3-28.2)
HDL	7.8 (7.4–8.6)	9.1 (7.8–9.8)	7.8 (7.2–8.9)	14.1 (13.2–15.9)	8.7 (8.1–9.3)	9.7 (9.1–10.9)	10.2 (9.3–11.1)	9.6 (8.9–10.2)	9.2 (8.8-9.8)
HDW	7.3 (6.6–7.8)	8.8 (7.3–9.7)	7.3 (6.4–8.2)	12.0 (11.2–12.6)	8.3 (7.6–9.2)	9.5 (8.8–10.4)	9.9 (9.1–10.5)	9.5 (9.0–10.0)	8.8 (7.9-9.8)
SNT	3.2 (3.0–3.6)	3.6 (3.0–4.1)	3.0 (2.0–3.2)	5.0 (4.4–5.7)	3.5 (3.1–3.9)	3.9 (3.3–4.5)	4.1 (2.4–4.6)	3.7 (3.3–4.2)	3.8 (3.4-4.3)
EYE	2.4 (2.0–2.8)	2.9 (2.3–3.4)	2.7 (2.3–3.1)	5.1 (4.8–5.4)	2.9 (2.8–3.3)	3.3 (3.0–3.5)	3.6 (3.2–4.0)	3.3 (3.2–3.4)	3.2 (2.9-3.5)
IOD	2.8 (2.4–3.1)	3.0 (2.4–3.5)	2.6 (2.4–2.9)	4.1 (3.9–4.5)	2.9 (2.4–3.3)	3.3 (2.9–3.6)	3.4 (2.9–3.9)	3.2 (3.0–3.5)	3.1 (2.8-3.5)
TMP	1.3 (1.1–1.6)	1.5 (0.9–1.9)	1.2 (0.8–1.5)	2.2 (2.1–2.4)	1.4 (1.1–1.7)	1.7 (1.6–2.0)	1.7 (2.9–3.9)	1.7 (1.5–1.8)	1.6 (1.4-2.0)
TEY	0.8 (0.6–1.0)	1.0 (0.4–1.4)	0.7 (0.5–1.0)	1.7 (1.3–2.0)	1.9 (0.7–1.2)	1.2 (0.9–1.5)	1.2 (0.8–1.7)	1.1 (0.9–1.3)	0.9 (0.7-1.2)
TIB	9.3 (8.9–10.0)	10.5 (8.1–11.3)	9.6 (9.1–10.4)	16.5 (15.9–17.2)	10.7 (10.2–11.4)	12.5 (11.8–13.0)	13.2 (12.3–14.3)	12.6 (11.6–13.3)	10.9 (10.4-11.7)
EN	1.7 (1.5–2.0)				2.0 (1.8–22)	2.4 (2.0–2.9)	2.5 (2.2–2.9)	2.5 (2.3–2.9)	2.4 (2.2-2.8)
IN	2.3 (2.1–2.5)				2.2 (2.0–2.5)	2.8 (2.5–3.1)	2.7 (2.4–3.1)	2.4 (2.3–2.6)	2.3 (2.1-2.7)
NS	1.4 (1.2–1.6)				1.3 (1.1–1.6)	1.6 (1.2–1.9)	1.7(1.5–1.9)	1.3 (1.1–1.4)	1.5 (1.2-1.8)
ML	4.8 (4.6–4.9)	5.3 (5.0–5.6)	4.7 (4.5–5.0)	8.4 (7.8–8.9)	5.7 (5.4–6.1)	6.7 (6.3–6.9)	6.9 (6.4–7.4)	6.7 (6.0–7.3)	5.7 (5.2-6.1)
PL	9.2 (8.1–9.8)	9.6 (8.1–10.4)	9.0 (8.7–9.2)	15.8 (15.0–16.3)	10.3 (9.4–11.4)	12.0 (11.1–12.6)	12.3 (11.1–13.5)	11.7 (10.1–12.6)	10.0 (9.4-10.7)
PEC	0.6 (0.5–0.8)	1.1 (0.8–1.6)	0.9 (0.7–1.3)		1.0 (0.7–1.3)	1.2 (0.9–1.7)	1.1 (0.7–1.9)	1.0 (0.9–1.0)	1.1 (0.8-1.3)
HDL/HDW	1.06 (1.05–1.11)	1.05 (0.96–1.07)	1.08 (0.97–1.13)	1.14 (1.12–1.31)	1.05 (0.89–1.11)	1.02 (0.96–1.13)	1.04 (0.96–1.15)	0.99 (0.99–1.02)	1.07 (1.00-1.11)
HDL/SVL	0.37 (0.36–0.40)	0.39 (0.36–0.42)	0.38 (0.35–0.39)	0.42 (0.38–0.47)	0.38 (0.37–0.41)	0.38 (0.35–0.39)	0.37(0.34–0.40)	0.38 (0.37–0.38)	0.38 (0.36-0.39)
TIB/SVL	0.45 (0.42–0.48)	0.44 (0.42–0.50)	0.46 (0.45–0.48)	0.50 (0.48–0.50)	0.47 (0.44–0.49)	0.49 (0.45–0.51)	0.48(0.45–0.52)	0.50 (0.48–0.50)	0.45 (0.43-0.48)
PEC/SVL	0.03 (0.02–0.04)	0.04 (0.03–0.07)	0.04 (0.03–0.06)		0.04 (0.03–0.06)	0.04 (0.03–0.07)	0.04 (0.03–0.07)	0.04 (0.04–0.04)	0.04 (0.03-0.05)
Weight in life (g)	0.9 (0.8–1.0)	0.9 (0.5–1.4) (n=4)			1.0 (1.0–1.2)				

TABLE 6. Measurements (mm) of female *Leptolalax applebyi* species group. Abbreviations defined in text.

	L. applebyi	*L. bidoupensis*	*L. pyrrhops*	*L. ardens* **sp. nov.** (Lineage 3)	*L. kalonensis* **sp. nov.** (Lineage 6)	*L. maculosus* **sp. nov.** (Lineage 8)	*L. tadungensis* **sp. nov.** (Lineage 9)
SEX	Female (n=9)	Female (n=3)	Female (n=2)	Female (n=1)	Female (n=3)	Female (m=1)	Female (n=1)
SVL	24.0(21.7–26.4)	29.0 (28.3–29.4)	30.3–33.9	24.5	26.9 (28.9–30.6)	27.0	32.1
HDL	8.7 (8.2–9.5)	10.1 (9.8–10.5)	12.0–14.2	9.1	11.1 (10.8–11.5)	9.2	10.1
HDW	8.2 (7.4–8.8)	9.6 (9.3–9.8)	11.1	8.7	10.0 (10.8–11.5)	9.1	10.6
SNT	3.5 (3.2–3.8)	3.8 (3.8–3.9)	4.8–5.2	3.7	4.3 (4.1–4.5)	3.3	3.9
EYE	2.9 (2.7–3.3)	3.0 (2.7–3.5)	4.5–4.8	3.2	3.7 (3.4–4.0)	3.2	3.1
IOD	2.8 (2.4–3.2)	3.2 (3.1–3.5)	3.8–4.0	2.7	3.5 (3.3–3.9)	3.1	3.8
TMP	1.4 (1.2–1.6)	1.8 (1.6–1.8)	1.9–2.0	1.5	1.7 (1.6–1.9)	1.8	1.8
TEY	0. 8(0.5–1.2)	1.2 (0.6–1.5)	1.4–1.7	0.9	1.2 (1.1–1.5)	1.1	1.2
TIB	10.1 (9.5–10.5)	11.4 (10.9–12.2)	15.5–16.0	11.1	13.7 (13.4–13.9)	12.4	12.3
EN	1.9 (1.6–2.1)			1.7	2.6 (2.3–2.7)	2.4	2.7
IN	2.5 (2.1–2.8)			2.6	3.0 (2.8–3.2)	2.1	3.2
NS	1.4 (1.1–1.5)			1.5	1.6 (1.4–1.7)	1.2	1.7
ML	5.2 (4.9–10.3)	5.8 (5.5–6.4)	7.9–8.9	5.7	7.2 (6.9–7.5)	6.6	6.7
PL	9.8 (9.4–10.3)	10.9 (10.5–11.3)	14.3–15.8	10.9	12.3 (11.5–13.7)	12.0	12.7
PEC	0.9 (0.8–1.0)	1.3 (1.2–1.4)		1.1	1.1 (0.9–1.2)	1.0	1.7
HDL/HDW	1.06 (1.05–1.10)	1.06 (1.06–1.07)	1.08–1.27	1.05	1.09 (1.07–1.14)	1.01	0.95
HDL/SVL	0.36 (0.34–0.38)	0.35 (0.34–0.36)	0.40–0.42	0.37	0.37 (0.36–0.39)	0.34	0.31
TIB/SVL	0.41 (0.39–0.48)	0.39 (0.38–0.41)	0.47–0.51	0.45	0.46 (0.46–0.47)	0.46	0.38
PEC/SVL	0.04 (0.03–0.04)	0.05 (0.04–0.05)		0.04	0.04 (0.03–0.05)	0.04	0.05
Weight in life (g)	1.2 (0.8–1.8) (n=7)	1.8 (1.4–2.2) (n=2)		1.5			

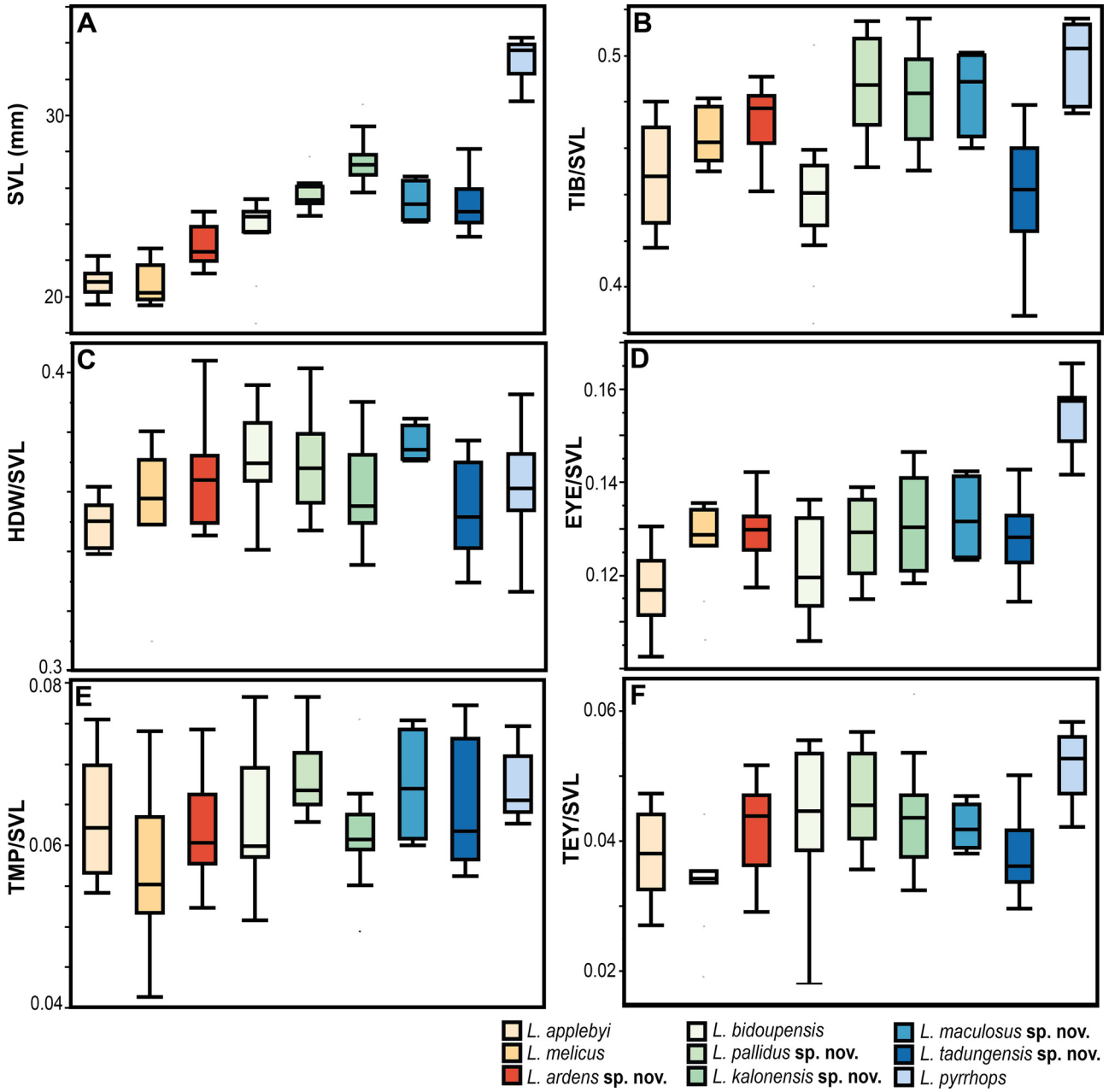

FIGURE 4. Morphometric variation and differentiation among adult male frogs in the *Leptolalax applebyi* group. Boxplots of (A) SVL, (B) relative tibia length (TIB/SVL), (C) relative pectoral gland size (PEC/SVL) and (D) relative tibia length (TIB/SVL) of adult males in each molecular lineage. For all boxplots, horizontal lines within each box represent the median and boxes encompass the 75th and 25th quartiles.

***Leptolalax ardens* sp. nov.**
Figs. 7D, 9A, 10.

Holotype. VNMN 04707/AMS R 176454, adult male, calling on clay bank 1.5 m from headwaters of 1–2m wide rocky, medium gradient, high–flow stream in evergreen forest in Kon Ka Kinh National Park, Gia Lai Province, Vietnam (14.2258° N, 108.3230° E; 1162 m elevation, Fig. 1, Fig 9E). Collected at 19:30 h on 21 August 2011 Jodi J. L. Rowley, Vinh Quang Dau, Huy Duc Hoang, Luong Thi Nguyen, Tan Thanh Le, Dinh Djung, and Y H'Jun.

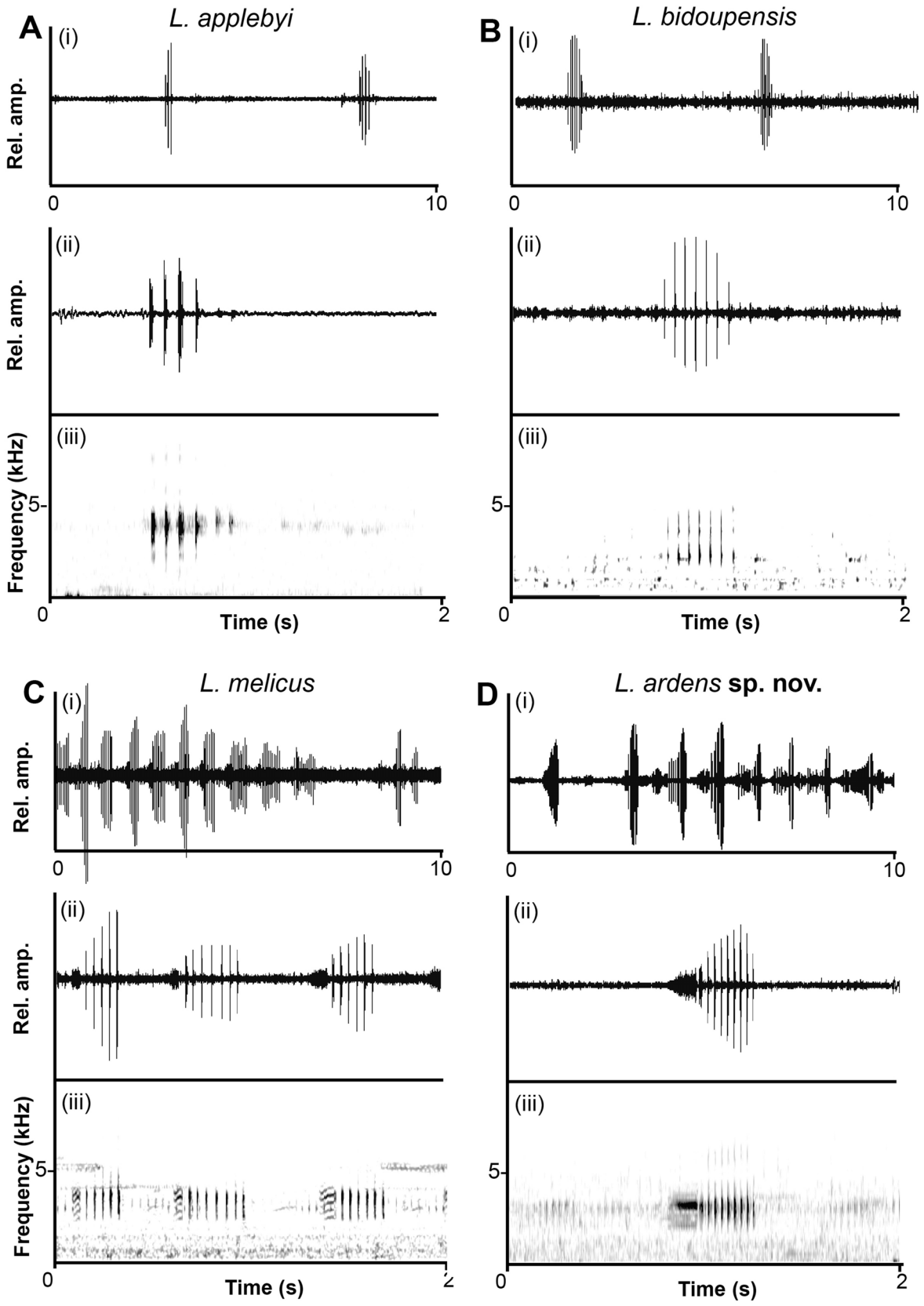

FIGURE 5. Advertisement calls of species in the *Leptolalax applebyi* group minus *L. pyrrhops* (i) 10 s waveform of relative amplitude (Rel. amp.) over time, (ii) waveform and (iii) corresponding 2 s spectrogram of representative call expanded from first section shown in i for (A) *L. applebyi* holotype AMS R 171703, (B) *L. bidoupensis* paratype UNS 00101/AMS R 173135, (C) *L. melicus* holotype MVZ 258198, and (D) *L. ardens* **sp. nov**. paratype UNS 00534/AMS R 176466. For ambient temperatures during recordings, see Table 4.

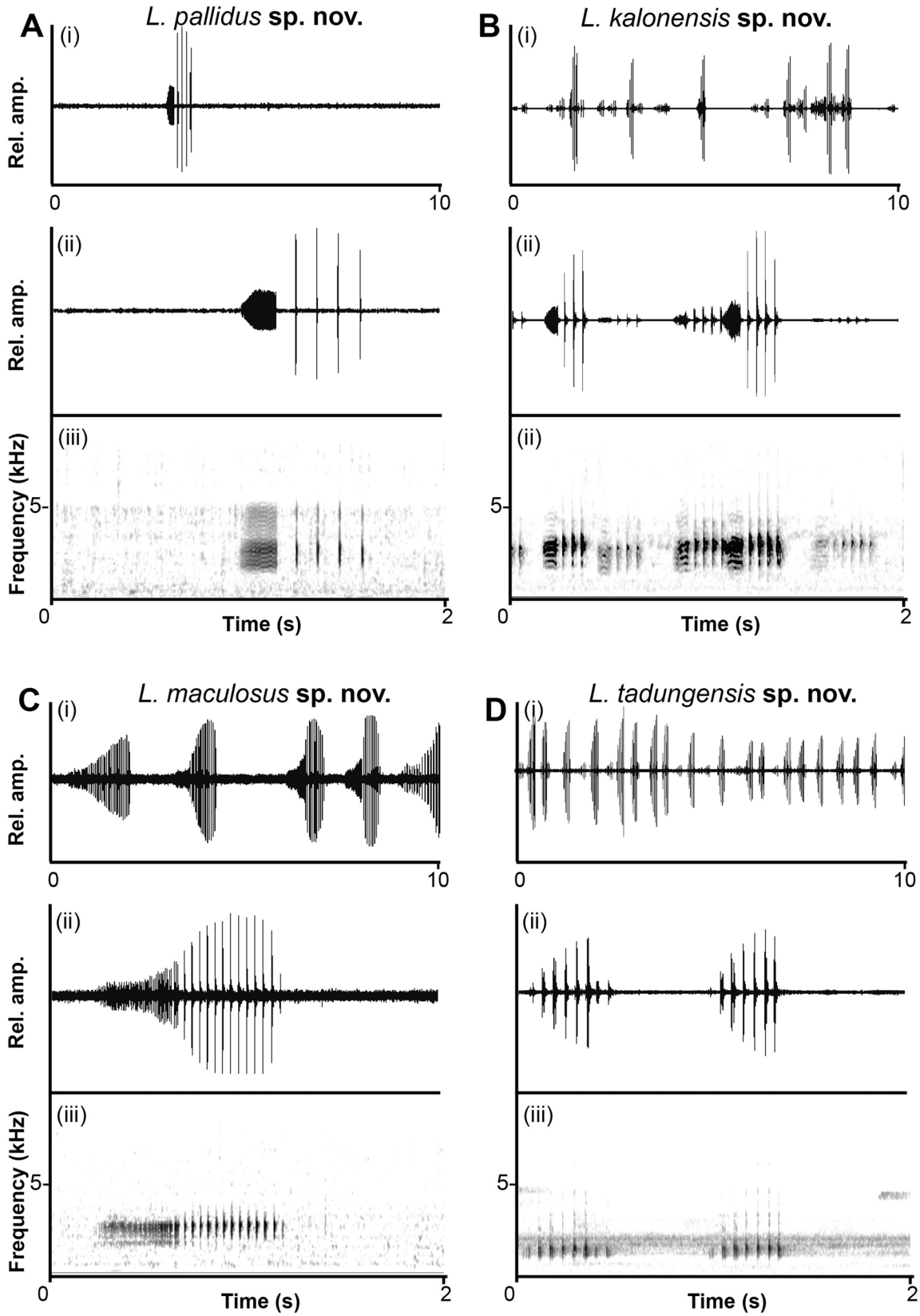

FIGURE 6. Advertisement calls of species in the *Leptolalax applebyi* group minus *L. pyrrhops* (i) 10 s waveform of relative amplitude (Rel. amp.) over time, (ii) waveform and (iii) corresponding 2 s spectrogram of representative call expanded from first section shown in i for (A) *L. pallidus* **sp. nov**. holotype UNS00510, (B) *L. kalonensis* **sp. nov**. paratype IEBR A.2014.21, (C) *L. maculosus* **sp. nov**. holotype UNS 00513, (D) *L. tadungensis* **sp. nov**. AMS R 177666. For ambient temperatures during recordings, see Table 4.

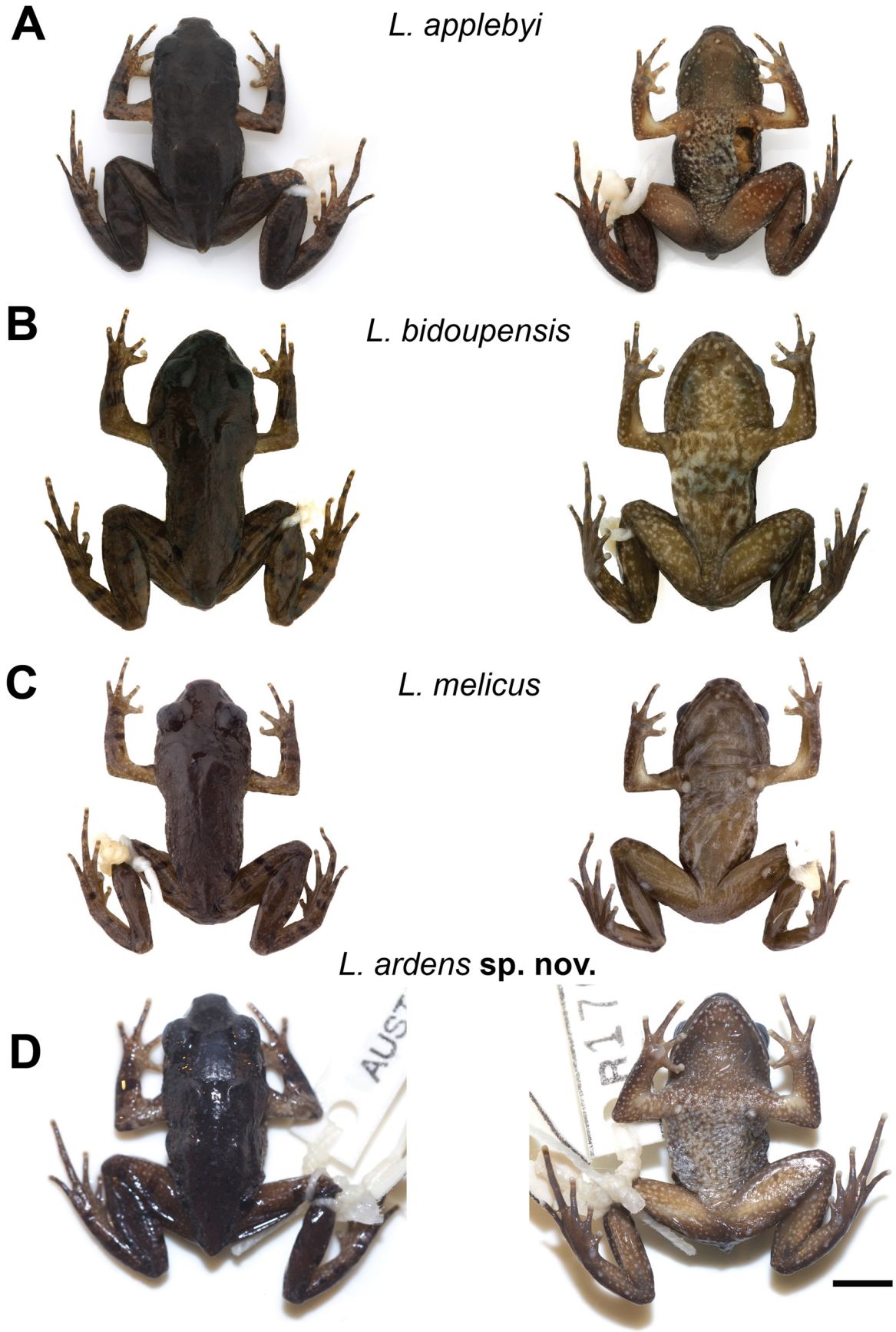

FIGURE 7. Dorsal and ventral views of holotypes of (A) *L. applebyi* AMS R 171703, (B) *L. bidoupensis* AMS R 173133, (C) *L. melicus* MVZ 258198, (D) *L. ardens* **sp. nov**. VNMN 04707/ AMS R 176454.

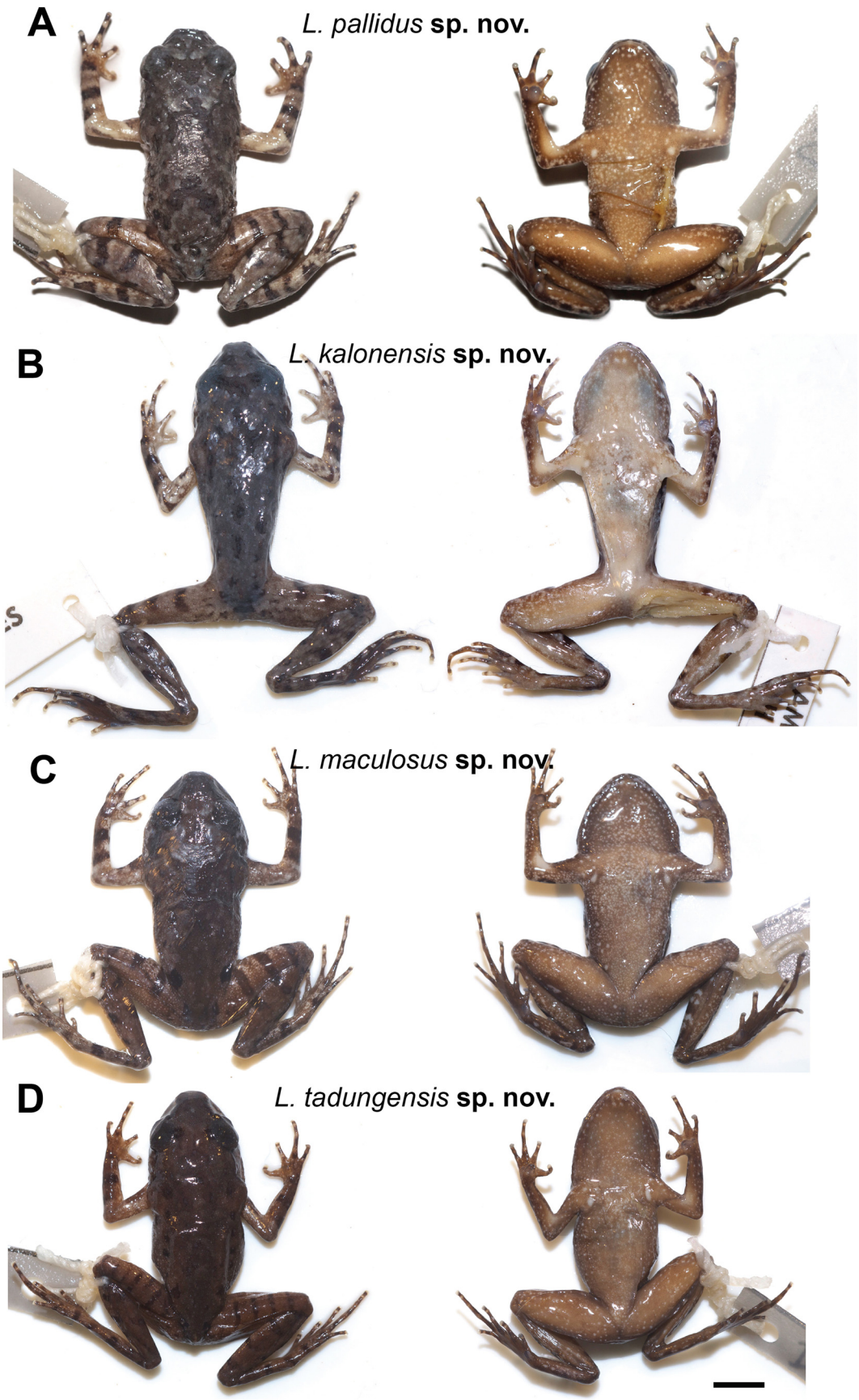

FIGURE 8. Dorsal and ventral views of holotypes of (A) *L. pallidus* **sp. nov**. UNS00510, (B) *L. kalonensis* **sp. nov**. IEBR A.2014.14, (C) *L. maculosus* **sp. nov**. UNS00513, (D) *L. tadungensis* **sp. nov**. UNS00516. Scale bar = 5 mm.

Paratypes. AMS R 176452–176453, two adult males (both calling), and VNMN 04708/AMS R 176455–VNMN 04710/AMS R 176457, three adult males (not observed calling), collected on same date and locality as holotype. VNMN 04711/AMS R 176458, adult female (gravid) and VNMN 04712/AMS R 176459 adult male (calling), collected at 19:55 h on 23 August 2011 in evergreen forest in Kon Ka Kinh National Park, Gia Lai Province, Vietnam (14.2263º N, 108.3345º E; 1450 m elevation). UNS 00530/AMS R 176460–UNS 00532/176462, AMS R 176463, AMS R 176464, UNS 00533/176465, UNS 00534/AMS R 176466, 176467, and NCSM 79650, 9 adult males, collected at night on 24 August 2011 in swampy area with small rocky stream in evergreen forest in Kon Ka Kinh National Park, Gia Lai Province, Vietnam (14.2197 º N, 108.3207 º E; 1041 m elevation). All specimens were collected by Jodi J. L. Rowley, Vinh Quang Dau, Huy Duc Hoang, Luong Thi Nguyen, Tan Thanh Le, Dinh Djung, and Y H'Jun.

Etymology. The specific name "*ardens*", meaning burning, fiery, shining, or brilliant, is used as an adjective in reference to the bold and conspicuous coloration of this species compared to other species in the group.

Diagnosis. Assigned to the genus *Leptolalax* on the basis of the following characters: small size, rounded finger tips, the presence of an elevated inner palmar tubercle not continuous to the thumb, presence of macroglands on body (including supra–axillary, pectoral, femoral and ventrolateral glands), the absence of vomerine teeth, the presence of tubercles on eyelids, and anterior tip of snout with pale vertical bar (Dubois 1983; Lathrop *et al*. 1998; Delorme *et al*. 2006). *Leptolalax ardens* **sp. nov.** is distinguished from its congeners by a combination of (1) supra–axillary and ventrolateral glands present; (2) dark brownish red ventral surface with white speckling; (3) small SVL for the genus (21.6.1–24.7 mm in 15 adult males, 24.5 mm in one female); (4) toes lacking webbing and lateral fringes; (5) tibia length 44–49% of SVL in males; (6) pectoral gland 3.5–5.6% of SVL in males, (7) mostly smooth dorsum, (8) iris dark coppery brown, (9) distinct black supratympanic line present, (10) an advertisement call with 3–10 notes with the first, introductory note encompassing one–third of each call.

Description of holotype. Head width equal to head length; snout slightly truncate in dorsal view and rounded in profile, projecting slightly beyond margin of the lower jaw; nostril closer to snout than to eye; canthus rostralis indistinct, gently rounded; lores sloping; pupil vertical; eye diameter smaller than snout length; tympanum distinct, round, diameter smaller than that of the eye; tympanic rim elevated relative to skin of temporal region; vomerine teeth absent; pineal ocellus absent; vocal sac openings slit–like, located posteriolaterally on floor of mouth; tongue wide with broad, shallow notch at posterior tip; supratympanic ridge distinct, running from eye to axillary gland. Tips of fingers rounded, very slightly swollen; 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 and dermal fringes absent. Tips of toes like fingers; relative toe length I < II < V < III < IV; subarticular tubercles absent, replaced by dermal ridges; large, oval inner metatarsal tubercle present, outer metatarsal tubercle absent; toe webbing rudimentary; lateral fringes absent. Tibia 48% of snout–vent length; tibiotarsal articulation reaching beyond tip of snout. Skin on dorsum mostly smooth with only tiny, barely raised tubercles; ventral skin smooth; pectoral gland small, oval, 0.8 mm diameter; femoral gland small, oval, approximately 0.5 mm diameter, on posteroventral surface of thigh, closer to knee than to vent; supra–axillary gland oval, raised, 0.9 mm diameter. Ventrolateral glands forming an indistinct line.

Colour of holotype in life. Dorsal surface brown with irregular, darker brown blotch down back; dark interorbital bar with pale cream edging anteriorly; two small, pale markings between axilla. Blackish brown line along canthus rostralis through eye, and continuing below supratympanic ridge, terminating above axilla, encompassing nare and most of tympanum; transverse dark brown bars on dorsal surface of thighs, tibia, tarsus, lower arms, fingers and toes; elbows and upper arms orange; large, black blotch on posterior flank and numerous, smaller black spots on sides from groin to axilla (Fig. 10A,C). Upper arms pale coppery orange. Dark brownish ventral surface with white speckling on entire ventral surface including throat, arms and legs; ventral margin of throat bearing broken row of slightly larger white spots. Supra-axillary gland copper; femoral glands white; pectoral glands white, ventrolateral glands white. Iris brown; minute, black reticulations throughout.

Colour of holotype in preservative. Dorsum relatively uniformly dark brown; dorsal surface of brachium, fingers and toes paler brown (Fig. 7D). Ventral surface of chest and thighs slightly medium brown with white speckles; throat dark brown speckled with white; and belly white speckled with brown. Macroglands creamy white.

Measurements (mm). Holotype: SVL 22.0, HDL 9.0, HDW 8.9, SNT 3.4, EYE 2.9, IOD 2.4, TMP 1.6, TEY 0.8, TIB 10.5, EN 2.0, IN 2.5, NS 1.3, ML 5.7, PL 10.8, weight in life 1.1g

Variation. Measurements of the type series are shown in Tables 2–3 and representative photographs of paratypes are shown in Figure 10. Some specimens (VNMN 04711/AMS R 176458– VNMN 04712/1764589)

have more clumped white speckling on the venter. UNS 00531/AMS R 176461 has a paler brown venter with barely distinct brown mottling. AMS R 176453, VNMN 04709/AMS R 176456, VNMN 04710/AMS R 176457, UNS 00532/AMS R 176462, AMS R 176463, UNS 00533/AMS R 176465, UNS 00534/AMS R 176466, have a distinctly pale line anterior to dark brown interorbital bar. The degree of black dorsolateral spots/flecks varies, pale edged marbling also visible on dorsum of some specimens, especially AMS R 176457, UNS 00532/AMS R 176462, UNS 00533/AMS R 176465.

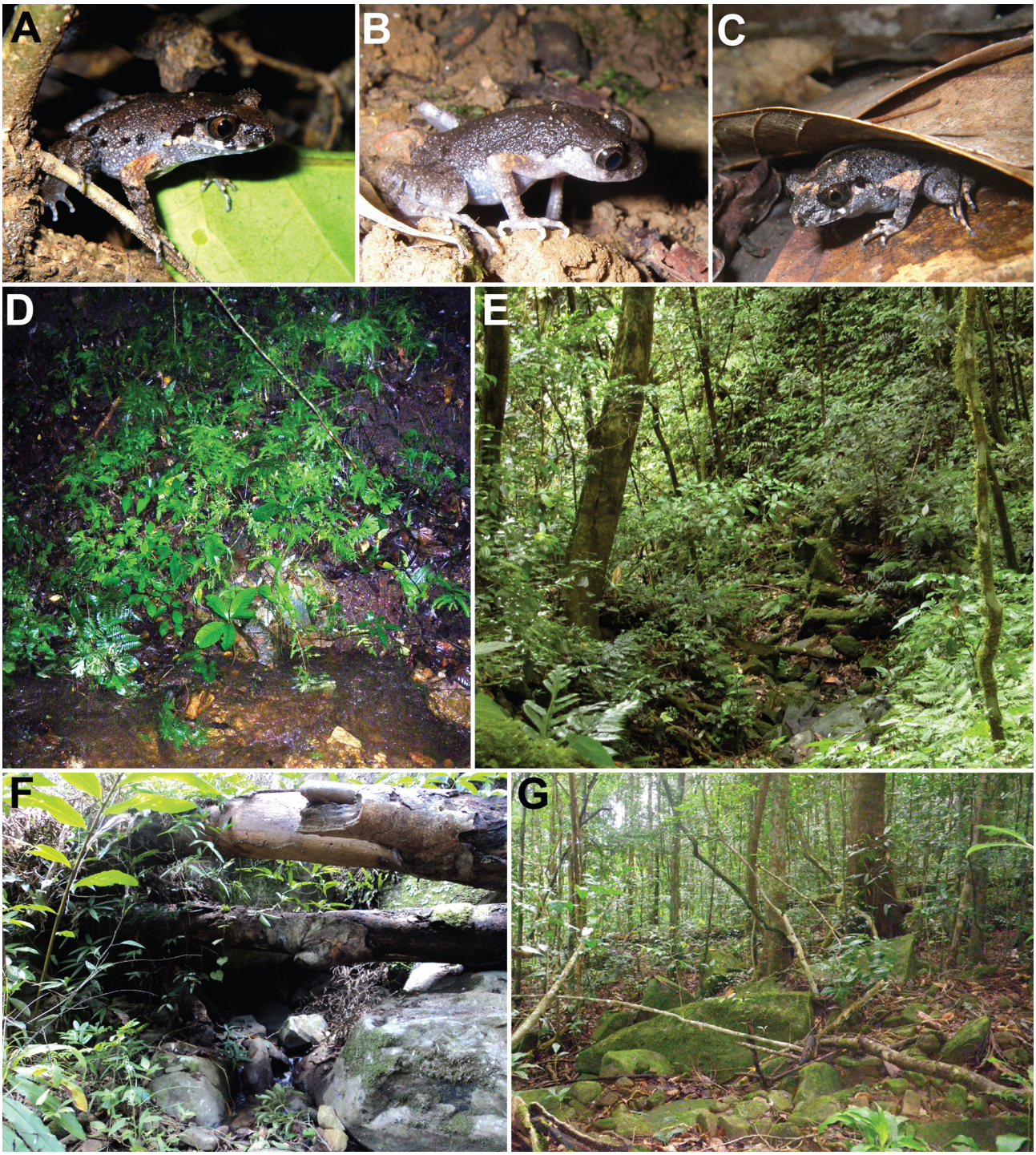

FIGURE 9. Calling sites and representative habitats of species in the *Leptolalax applebyi* group. (A) *L. ardens* **sp. nov.,** (B) *L. kalonensis* **sp. nov.** , (C) *L. maculosus* **sp. nov.**. (D) stream in Kon Ka Kinh National Park, Gia Lai Province, where *L. ardens* **sp. nov.** males were observed 1-2 m from stream, calling under leaf-litter, (E) downstream from dry section of stream in Bidoup Nui Ba National Park, Lam Dong Province, where *L. pallidus* **sp. nov**. were observed calling, (F) dry stream bed in Song Luy Watershed Forest, Binh Thuan Province, where calling *L. kalonensis* **sp. nov.** were collected, and (G) dry stream bed in Ta Dung Forest, Dak Nong Province, where *L. tadungensis* **sp. nov.** were calling and collected.

FIGURE 10. *Leptolalax ardens* **sp. nov**. in life (A) male holotype VNMN 04707/AMS R 176454, (B) male paratype AMS R 176467, (C) venter of male holotype VNMN 04707/AMS R 176454, (D) male paratype UNS 00534/AMS R 176466.

Advertisement call. Call descriptions are based on the calls of seven individuals, recorded at 21.4–24.7 ºC ambient temperature. Calls were an average of 239 ms in duration and consisted of 3–10 notes (Table 4, Fig. 5D). Calls were highly amplitude modulated, with amplitude peaking towards the end of each call. Calls contained 3–10 notes and introductory notes were present in most calls. Introductory notes were 25–41% of the call duration, contained up to 54 pulses. Non-introductory notes contained 1–3 pulses. Notes were repeated an average of 20 notes/s. The average dominant frequency was 3.3 kHz, spread more widely (~2.0–7.6 kHz) in non-introductory notes. Harmonics were weakly present at ~ 6, 9, and 12 kHz, and a fundamental frequency was not visible. To the human ear, the advertisement call of *L. ardens* **sp. nov.** is a weak squeak followed by a rasping, similar to an orthopteran.

Ecology. All specimens of *Leptolalax ardens* **sp. nov.** were found in evergreen forest between 1,041–1,450 m elevation in Kon Ka Kinh National Park. Males were heard faintly calling on the forest floor, adjacent to small streams or seeps (Figure 9D).

Distribution. *Leptolalax ardens* **sp. nov.** is only known from Kon Ka Kinh National Park, in Gia Lai Province, Vietnam.

Comparisons. *Leptolalax ardens* **sp. nov.** differs from all other *Leptolalax* species in mainland Southeast Asia on the basis of morphology, and from all congeners in the region for which comparable data is available on the basis of molecular and acoustic data.

The new species differs from *L. aereus* by ventral coloration, body size and the presence of a black supratympanic line, from *L. bourreti* by ventral coloration and body size, from *L. botsfordi* by male body size and relative body weight (0.41–0.47 versus 0.75–0.94 g/mm), from *L. croceus* by ventral coloration, presence of black

supratympanic line, iris coloration and skin texture; from *L. eos* by ventral coloration, male body size, iris coloration and lateral fringes on toes; from *L. firthi* by ventral coloration, male body size, presence of black supratympanic line, iris coloration, male skin texture and lateral fringes on toes; from *L. fuliginosus* by ventral coloration, male body size and iris coloration; from *L. heteropus* by ventral coloration and male body size; from *L. kecil* by ventral coloration, male body size, and iris coloration; from *L. melanoleucus* by ventral coloration, male body size, and iris coloration; from *L. minimus* by ventral coloration and male body size; from *L. nahangensis* by ventral coloration, male body size and iris coloration; from *L. nyx* by ventral coloration and male body size, from *L pelodytoides* by ventral coloration and male body size; from *L. platycephalus* by ventral coloration and male body size; from *L. pluvialis* by ventral coloration; from *L. solus* by ventral coloration, male body size and iris coloration; from *L. sungi* by ventral coloration, male body size, presence of black supratympanic line, iris coloration and skin texture; from *L. tuberosus* by ventral coloration, presence of black supratympanic line, iris coloration and skin texture; from *L. ventripunctatus* by ventral coloration, male body size, iris coloration and skin texture; and from *L. zhangyangpingi* by ventral coloration, male body size, presence of black supratympanic line, and iris coloration. See Table 8 for details.

From members of the *L. applebyi* group, *L. ardens* **sp. nov**. differs from all species by at least one morphological character (all following morphometric differences refer to males only). The new species differs from *L. applebyi* by having a significantly larger body size (Wilcoxon post-hoc $Z=3.7$, $p<0.001$), larger relative tibia length (Wilcoxon post-hoc $Z=2.3$, $p=0.020$), larger relative head width (Wilcoxon post-hoc $Z=2.3$, $p=0.023$), larger relative eye diameter (Wilcoxon post-hoc $Z=3.2$, $p=0.002$) and larger pectoral gland size (Wilcoxon post-hoc $Z=3.81622$, $p<0.001$). *L. ardens* **sp. nov**. differs from *L. bidoupensis* by having a smaller SVL (Wilcoxon post-hoc $Z= -2.0$, $p=0.048$), larger relative tibia length (Wilcoxon post-hoc $Z=3.2$, $p=0.001$), larger relative eye diameter (Wilcoxon post-hoc $Z=2.1$, $p=0.038$) and having a relatively uniform iris coloration (versus reddish in upper and silvery gold below). *L. ardens* **sp. nov**. differs from *L. melicus* by having a larger SVL (Wilcoxon post-hoc $Z= -3.3$, $p<0.001$), and larger relative distance between the tympanum and eye (Wilcoxon post-hoc $Z= -2.5$, $p=0.011$). *L. ardens* **sp. nov**. differs from *L. pyrrhops*, by having a smaller and non-overlapping body size (Wilcoxon post-hoc $Z= 3.7$, $p<0.001$), and smaller relative tympanum diameter (Wilcoxon post-hoc $Z=2.6$, $p=0.009$), and distance between tympanum and eye (Wilcoxon post-hoc $Z=2.7$, $p=0.006$), and larger relative eye size (Wilcoxon post-hoc $Z=3.6$, $p<0.001$; although differences between the latter three measurements may be confounded by inter-observer bias). *L. ardens* **sp. nov**. differs from *L. pallidus* **sp. nov**. by having a smaller SVL (Wilcoxon post-hoc $Z= -3.8$, $p<0.001$), smaller relative tympanum diameter (Wilcoxon post-hoc $Z= -2.7$, $p=0.007$), a distinct black (versus dark brown and less distinct) supratympanic line and mostly smooth skin texture (versus distinctly tuberculate dorsum). *L. ardens* **sp. nov**. differs from *L. kalonensis* **sp. nov.** by having a non-overlapping, smaller body size (Wilcoxon post-hoc $Z= 4.7$, $p<0.001$). *L. ardens* **sp. nov**. differs from *L. maculosus* **sp. nov.** by having a smaller body size (Wilcoxon post-hoc $Z=2.8$, $p=0.006$). *L. ardens* **sp. nov**. differs from *L. tadungensis* **sp. nov.** by having a smaller body size (Wilcoxon post-hoc $Z= 3.4$, $p<0.001$) and larger relative tibia length (Wilcoxon post-hoc $Z=-3.0$, $p=0.003$). See Table 4 and Fig. 4.

The male advertisement call of *L. ardens* **sp. nov.** differs from all members of the *L. applebyi* group with the exception of *L. kalonensis* **sp. nov**. From *L. applebyi* the call of the new species differs by having a longer introductory note and note repetition rate. From *L. bidoupensis*, the call of *L. ardens* **sp. nov.** differs by having an introductory note in most calls and having a higher dominant frequency. From *L. melicus*, the call of *L. ardens* **sp. nov.** differs by having a lower dominant frequency. From *L. pyrrhops* the call of *L. ardens* **sp. nov.** appears to differ by having a higher dominant frequency. From *L. pallidus* **sp. nov.** the call of *L. ardens* **sp. nov.** differs by having a shorter call duration,a higher average number of pulses in the introductory note, a higher note repetition rate and a higher dominant frequency. From *L. maculosus* **sp. nov.** the call of *L. ardens* **sp. nov.** differs by having a shorter call duration, a higher number of notes per call, a distinct introductory note, and higher dominant frequency. From *L. tadungensis* **sp. nov.** the call of *L. ardens* **sp. nov.** differs by having a relatively long introductory note. No clear differences between the call of *L. ardens* **sp. nov.** and *L. kalonensis* **sp. nov.** could be determined, perhaps in part due to the limited sample size (n=1) for *L. kalonensis* **sp. nov.** See Table 7 and Figs. 5–6.

Leptolalax ardens **sp. nov.** differs from all species within the *L. applebyi* group by >4.5% divergence at the 16S gene fragment examined. Interspecific variation in three *L. ardens* **sp. nov.** collected from ~2 km apart was 0%.

TABLE 7. Measurements of advertisement call parameters for species in the *Leptolalax applebyi* group. Parameter values are given as means (and ranges).

	L. applebyi	*L. bidoupensis*	*L. melicus*	*L. pyrrhops*	*L. ardens* **sp. nov.** (Lineage 3)	*L. pallidus* **sp. nov.** (Lineage 5)	*L. kalonensis* **sp. nov.** (Lineage 6)	*L. maculosus* **sp. nov.** (Lineage 8)	*L. tadungensis* **sp. nov.** (Lineage 9)
Av. call duration (ms)	304 (213–404)	368 (308–400)	222 (216–228)	254 (208–297)	239 (144–373)	673 (627–729)	201	907 (889–907)	291 (248–353)
# Notes/call	4.4 (3–6)	6.9 (5–8)	5.1 (4–7)	5.7 (5–6)	5.7 (3–10)	5.6 (4–7)	4.2 (4–5)	16.35 (7–38)	5.2 (4–7)
Introductory note	Present	Absent	Present	Present	Present (not all calls)	Present (short)	Present	Indistinct	Present
Av. % duration of introductory note	1 (3–9)	1 (1–2)	32 (24–42)	~17	32 (25–41)	25 (22–26)	29	21 (10–37)	6 (3–9)
Av. pulses in introductory notes	–	–	27 (16–37)	7 (5–12)	13 (0–54)	48 (37–63)	15	46 (12–88)	–
Av. pulses in non–introductory notes	3.1(1–5)	1	1(1–2)	1	1.1 (1–3)	1	1.1	1.2 (1–4)	1.7 (1–4)
Av. note repetition rate	11.3 (8.9–13.4)	16 (14.6–18)	18.2 (15.9–21.1)	18.6 (16.8–19.4)	19.8 (15.1–29.9)	6.8 (6.2–8.0)	16	16.5 (11.1–23.3)	14.3 (1.8–19.7)
Av. dominant frequency (kHz)	4.1 (3.9–4.3)	2.1 (1.9–2.3)	3.7 (3.7–3.8)	2.1 (1.9–2.2)	3.3 (3.1–3.4)	2.5 (2.4–2.7)	2.8	2.7 (2.7–2.8)	2.8 (2.6–3.1)
Temperature (ºC)	21.5	19.9 (19.0–20.4)	26.2 (26.1–26.2)	25	23.6 (21.4–24.7)	18.9 (14.0–21.4)	26.4	23.7 (23.3–24.1)	18.3 (12.9–22.3)
Individuals analysed	3	3	2	1	7	3	1	2	4

TABLE 8. *Leptolalax* species known from mainland Southeast Asia.

Species	Ventral Coloration	Male SVL (mm)	Distinct black supratympanic line	Iris colouration	Dorsal skin Texture	Wide lateral fringes on toes
L. aereus	White with pale brown speckling at margins	25.1–28.9	No	Uniformly bronze	Finely tuberculate	No
L. bourreti	Whitish	28.0–36.2	Yes	Copper above, golden below	Smooth – slightly shagreened	No
L. botsfordi	Reddish brown with white speckling	29.1–32.6	Yes	Uniformly brownish gold	Shagreened	No
L. croceus	Bright orange	22.2–27.3	No	Gold, more silver below	Highly tuberculate	No
L. eos	Creamy white with brown speckling at margins	33.1–34.7	No	Orange above, light gold below	Shagreened	Yes
L. firthi	Creamy white	26.4–29.2	No	Bright gold	Shagreened, more in males	Yes
L. fuliginosis	Dusty	28.2–30.0	Yes	Reddish orange above, gold below	Nearly smooth, few low tubercles	No
L. heteropus	Grey speckled with black	33 (topotypes 24.6–26.9)	Yes	-	Smooth	No
L. kecil	Dusky dotted with dark brown	19.3–20.5	Yes	Dark red	Shagreened	No (moderate)
L. melanoleucus	Large black markings on a white background	26.6–28.8	Yes	Orange above, silver below	Nearly smooth, few low tubercles	No
L. minimus	Whitish	25.6–31.4	Yes	-	Smooth	No
L. nahangensis	White with brown specking at margins	40.8	Yes	Uniformly gold	Nearly smooth, few low tubercles	No
L. nyx	Whitish with brown border	26.7–32.6	Yes	-	Nearly smooth, few low tubercles	No
L. pelodytoides	White, throat brown in males	27.5-32.3	Yes	-	Nearly smooth, few low tubercles	No
L. platycephalus	Light coloured and unpatterned except margins	35.1	Yes?	Orange red or reddish brown	-	No
L. pluvialis	Dirty white with dark brown marbling	21.3–22.3	Yes	Dark golden	Smooth	No
L. solus	White with dark brown specks	27.6	Yes	Dark red above, dark brown below	Weakly shagreened	No

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TABLE 8. (Continued)

Species	Ventral Coloration	Male SVL (mm)	Distinct black supratympanic line	Iris colouration	Dorsal skin Texture	Wide lateral fringes on toes
L. sungi	White, mottling at margins	48.3–52.7	No	Gold green	Shagreened	No
L. tuberosus	White or pale creamy orange with blackish grey specks or streaks	24.4–29.5	No	Gold	Highly tuberculate	No
L. ventripunctatus	Chest and belly covered with dark spots	25.5–28.0	Yes	Copper above, grey brown below	Longitudinal ridges	No
L. zhangyangpingi	White with brown specking at margins	45.8–52.5	No	Golden above, grey below	Nearly smooth, few low tubercles	No (moderate)
L. applebyi	Reddish brown with white speckling	19.6–22.3 (20.8)	Yes	Gold	Smooth	No
L. bidoupensis	Reddish brown with white speckling	18.5–25.4 (23.6)	Yes	Reddish above, silver below	Smooth	No
L. melicus	Reddish brown with white speckling	19.5–22.7(20.7)	Yes	Gold	Smooth	No
L. pyrrhops	Reddish brown with white speckling	30.8–34.3 (33.2)	Yes	Orange	Slightly shagreened	No
L. ardens **sp. nov**	Reddish brown with white speckling	21.3–24.7 (22.8)	Yes	Brown	Smooth – finely shagreened	No
L. pallidus **sp. nov**	Reddish brown with white speckling	24.5–27.7 (25.6)	No	Dark brown	Tuberculate	No
L. kalonensis **sp. nov**	Pale, speckled brown	25.8–30.6 (27.4)	Yes	Gold, some with bronze above	Smooth	No
L. maculosus **sp. nov**	Brown, less white speckling	24.2–26.6 (25.5)	Yes	Bronze	Smooth – finely shagreened	No
L. tadungensis **sp. nov**	Reddish brown with white speckling	23.3–28.2 (25.0)	Yes	Gold	Smooth	No

***Leptolalax pallidus* sp. nov.**
Figs. 8A, 11.

Holotype. UNS 00510, adult male, calling on plant leaf 0.1 m from ground, 1 m from 2–3 m wide rocky stream in evergreen forest, Bidoup Nui Ba National Park, Lam Dong Province, Vietnam. (12.1520 º N, 108.695º E; 1644 m elevation, Fig. 1, 9E). Collected at night on 27 June 2011 by Dao T. A. Tran and Duong T. T. Le.

Paratypes. UNS 00512, AMS R 177657, ZFMK 96599, three adult males collected on 26 July 2011 in in evergreen forest in Bidoup Nui Ba National Park, Lam Dong Province, Vietnam (12.1519º N, 108.6940º E; 1681 m elevation). UNS 00511, AMS R 177659, ZFMK 96598, three adult males collected on same date and location as holotype. AMS R 177658, collected on 27 June 2011 at same location as holotype. All specimens were collected by Dao T. A. Tran and Duong T. T. Le

Etymology. The specific name "*pallidus*", meaning pale, is used as an adjective in reference to the paler coloration and less distinct markings of this species, particularly in preservative, compared to other species in the group.

Diagnosis. Assigned to the genus *Leptolalax* on the basis of the following characters: small size, rounded finger tips, the presence of an elevated inner palmar tubercle not continuous to the thumb, presence of macroglands on body (including supra–axillary, pectoral, femoral and ventrolateral glands), the absence of vomerine teeth, the presence of tubercles on eyelids, and anterior tip of snout with pale vertical bar (Dubois 1983; Lathrop *et al*. 1998; Delorme *et al*. 2006). *Leptolalax pallidus* **sp. nov.** is distinguished from its congeners by a combination of (1) supra–axillary and ventrolateral glands present; (2) dark brownish red ventral surface with faint white speckling; (3) small SVL for the genus (24.5.1–27.7 mm in 8 adult males), (4) toes lacking webbing and lateral fringes; (5) tibia length 45–51% of SVL in males; (6) pectoral gland 3.4–6.7% of SVL in males, (7) tuberculate skin texture on dorsum, (8) iris copper in upper half, gold in lower half; (9) distinct black supratympanic line absent, (10) an advertisement call with 4–7 notes with the short introductory note encompassing a quarter of each call and only one note in non-introductory notes.

Description of holotype. Head width slightly subequal to head length; snout truncate in dorsal view and in profile, projecting slightly beyond margin of the lower jaw; nostril closer to snout than to eye; canthus rostralis indistinct, gently rounded; lores sloping; pupil vertical; eye diameter smaller than snout length; tympanum indistinct, round, diameter smaller than that of the eye; tympanic rim slightly elevated relative to skin of temporal region; vomerine teeth absent; pineal ocellus absent; vocal sac openings small, located posteriolaterally on floor of mouth; tongue wide with broad, shallow notch at posterior tip; supratympanic ridge distinct, running from eye to axillary gland. Tips of fingers rounded, very slightly swollen; relative finger lengths I < IV < II < III; nuptial pad absent; subarticular tubercles absent except at base of finger IV; a large, round inner palmar tubercle distinctly separated from small, laterally compressed outer palmar tubercle; finger webbing and dermal fringes absent. Tips of toes like fingers; relative toe length I < II < V < III < IV; subarticular tubercles absent, replaced by dermal ridges, distinct on base of toes II and III; large, oval inner metatarsal tubercle present, outer metatarsal tubercle absent; toe webbing rudimentary; lateral fringes absent. Tibia 51% of snout–vent length; tibiotarsal articulation reaching to anterior edge of eye. Skin on dorsum coarsely shagreened; ventral skin smooth; pectoral gland oval, 1.7 mm diameter; femoral gland oval, approximately 1.0 mm diameter, on posteroventral surface of thigh, closer to knee than to vent; supra–axillary gland oval, raised, 1.5 mm diameter. Ventrolateral glands discernible on right side only.

Colour of holotype in life. Dorsal surface brown with slightly darker interorbital bar with pale brown patches anteriorly and posteriorly; faint dark W-shaped marking between axilla (Fig. 11A). Darker brown line along supratympanic ridge, terminating above axilla, encompassing most of tympanum; transverse dark brown bars on dorsal surface of thighs, tibia, tarsus, lower arms, fingers and toes; elbows and upper arms paler brown; numerous, small dark brown spots on sides from groin to axilla. Dark brownish ventral surface with white speckling on ventral surfaces of throat, chest and belly, more sparse on legs and arms. Supra-axillary gland copper; femoral glands white; pectoral glands white, ventrolateral glands white. Iris copper in upper half, gold in lower half, black reticulations throughout.

Colour of holotype in preservative. Dorsum relatively uniform medium brown with darker interorbital bar and slightly paler posterior to this; dorsal surface of brachium, fingers and toes paler brown, dark brown/black banding on dorsal surface of tibiotarsus, antebrachium, hands and feet (Fig. 8A). Elbows and upper arms pale brown. Ventral surface medium brown with faint white speckles. Macroglands creamy white.

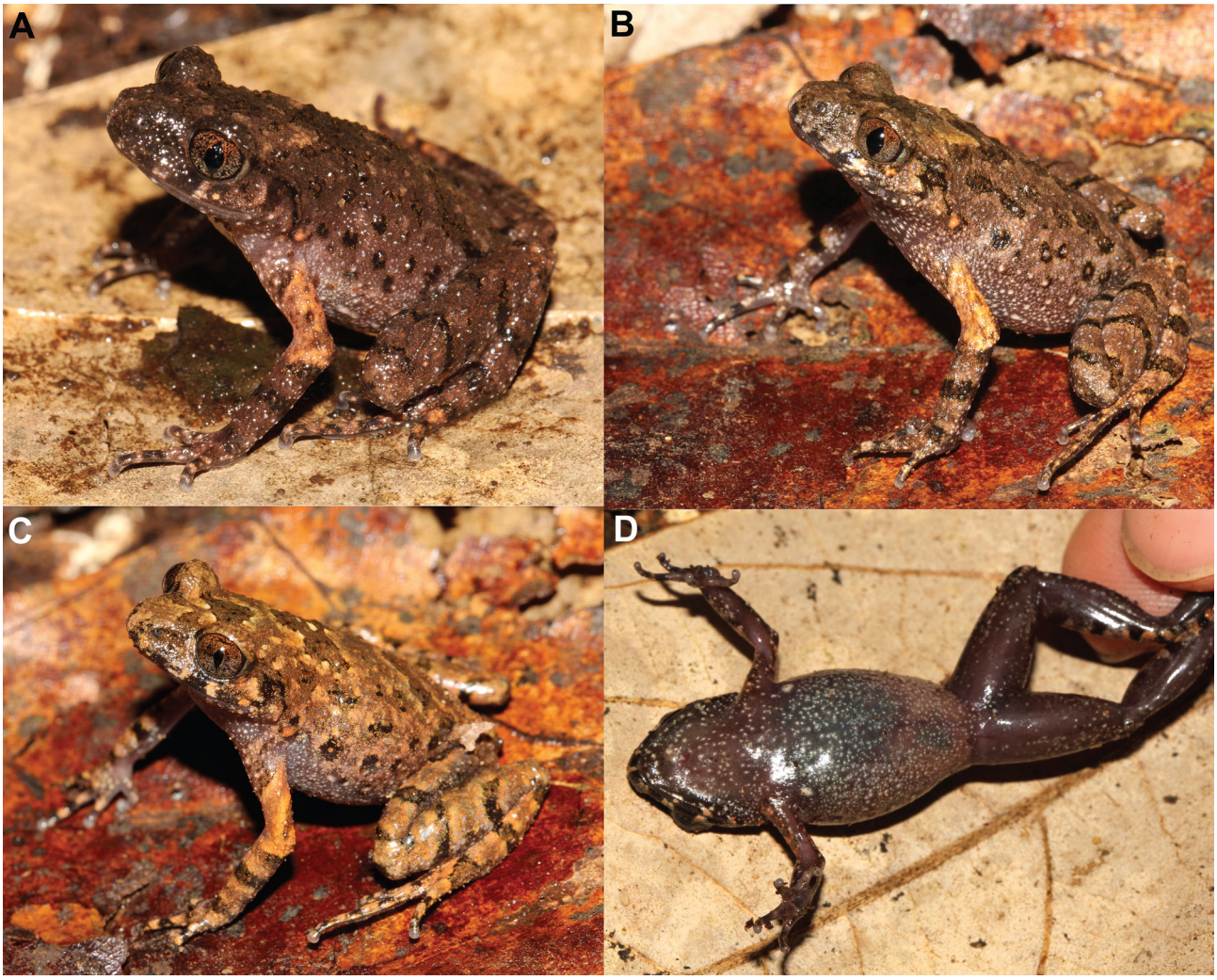

FIGURE 11. *Leptolalax pallidus* **sp. nov**. in life (A) male holotype UNS 00510, (B) male paratype AMS R 177657 (C) male paratype UNS 00512, (D) ventral surface male paratype UNS 00512.

Measurements (mm). Holotype: SVL 25.2, HDL 9.4, HDW 9.2, SNT 3.9, EYE 3.4, IOD 3.2, TMP 1.7, TEY 1.4, TIB 13.0, EN 2.5, IN 2.6, NS 1.2, ML 6.8, PL 12.6.

Variation. Measurements of the type series are shown in Tables 5–6 and representative photographs of paratypes are shown in Fig. 11. All specimens have a degree of darker brown patterning (mostly marbling but also some spots) on the dorsum and dark banding on the tibiotarsus and antebrachium, hands and feet, but both are more pronounced in UNS00512, AMS R 177657 and UNS00511. ZFMK 96599 has faint dark brown spots evenly distributed around tubercles on dorsum. UNS00510–00512 have more distinctly pale elbows in preservative. Size and distribution of white speckles on the venter varies a little between specimens, more clumped on chest in AMS R 177659 and ZFMK 96598. Skin texture less tuberculate in preservative than in life.

Advertisement call. Call descriptions are based on the calls of three individuals, recorded at 14.0–21.4 ºC ambient temperature. Calls were an average of 673 ms in duration and consisted of 4–7 notes (Table 7, Fig. 6A). Short introductory notes of low relative amplitude were present in all calls. Introductory notes were 22–26% of the call duration, contained up to 63 pulses. Non-introductory notes invariably contained a single pulse. Amplitude peaked towards the middle of the call. Notes were repeated an average of 6.8 notes/s. The average dominant frequency was 2.5 kHz. Harmonics were weakly present at ~7.3 kHz, and a fundamental frequency was not visible. To the human ear, the advertisement call of *L. pallidus* **sp. nov.** consists of a squelch followed by clicking.

Ecology. All specimens of *Leptolalax pallidus* **sp. nov.** were found in evergreen forest in Bidoup Nui Ba National Park between 1644–1681 m elevation. Males were located on the forest floor, on leaf-litter or rocky crevices and clay holes in the banks of a dry stream. Fig 9E.

Distribution. *Leptolalax pallidus* **sp. nov.** is only known from Gia Rich mountain in Bidoup Nui Ba National Park, only about 5 km from *L. bidoupensis*. The two species occur in continuous forest, with no obvious current biogeographic barrier between them.

Comparisons. *Leptolalax pallidus* **sp. nov.** differs from all other *Leptolalax* species in mainland Southeast Asia on the basis of morphology, and from all congeners in the region for which comparable data is available on the basis of molecular and acoustic data.

The new species differs from *L. aereus* by ventral coloration and iris coloration, from *L. bourreti* by ventral coloration, male body size, absence of black supratympanic line, skin texture and iris coloration, from *L. botsfordi* by male body size, absence of black supratympanic line, iris coloration and relative male body weight (0.42–0.50 versus 0.75–0.94 g/mm), from *L. croceus* by ventral coloration and iris coloration; from *L. eos* by ventral coloration, male body size, iris coloration and lateral fringes on toes; from *L. firthi* by ventral coloration, absence of black supratympanic line, iris coloration and lateral fringes on toes; from *L. fuliginosus* by ventral coloration, male body size, skin texture and iris coloration; from *L. heteropus* by ventral coloration, male body size, skin texture and absence of black supratympanic line; from *L. kecil* by ventral coloration, male body size, absence of black supratympanic line and iris coloration; from *L. melanoleucus* by ventral coloration, body size, absence of black supratympanic line, skin texture and iris coloration; from *L. minimus* by ventral coloration, skin texture and male body size; from *L. nahangensis* by ventral coloration, male body size, skin texture, absence of black supratympanic line and iris coloration; from *L. nyx* by ventral coloration, skin texture and absence of black supratympanic line, from *L pelodytoides* by ventral coloration and absence of black supratympanic line; from *L. platycephalus* by ventral coloration and male body size; from *L. pluvialis* by ventral coloration, body size, skin texture and absence of black supratympanic line; from *L. solus* by ventral coloration, absence of black supratympanic line, skin texture and iris coloration; from *L. sungi* by ventral coloration, male body size and iris coloration; from *L. tuberosus* by ventral coloration, presence of black supratympanic line, iris coloration and skin texture; from *L. ventripunctatus* by ventral coloration, absence of black supratympanic line, skin texture and iris coloration; and from *L. zhangyangpingi* by ventral coloration, male body size, skin texture and iris coloration. See Table 8 for details.

From members of the *L. applebyi* group, *L. pallidus* **sp. nov**. differs by at least one morphological character (all following morphometric differences refer to males only). The new species differs from *L. applebyi* by having a significantly larger and non-overlapping male body size (Wilcoxon post-hoc $Z=3.4$, $p<0.001$), larger relative tibia length (Wilcoxon post-hoc $Z=2.7$, $p=0.006$), larger relative head width (Wilcoxon post-hoc $Z=2.5$, $p=0.011$), larger relative diameter of the eye (Wilcoxon post-hoc $Z=2.3$, $p=0.024$), larger relative pectoral gland size (Wilcoxon post-hoc $Z=3.0$, $p=0.002$), indistinct, brown supratympanic line (versus distinct black supratypmanic line in *L. applebyi*) and tuberculate skin texture (versus mostly smooth in *L. applebyi*). *L. pallidus* **sp. nov**. differs from *L. bidoupensis* by having a significantly larger body size (Wilcoxon post-hoc $Z=2.7$, $p=0.006$), larger relative tibia length (Wilcoxon post-hoc $Z=3.0$, $p=0.002$), larger relative tympanum size (Wilcoxon post-hoc $Z=2.0$, $p=0.041$), dark brown iris (versus reddish upper and silver below), indistinct, brown supratympanic line (versus distinct black supratypmanic line in *L. bidoupensis*) and tuberculate skin texture (versus mostly smooth in *L. bidoupensis*). *L. pallidus* **sp. nov**. differs from *L. melicus* by having a significantly larger and non-overlapping male body size (Wilcoxon post-hoc $Z=-3.3$, $p<0.001$), larger length between eye and tympanum (Wilcoxon post-hoc $Z=-3.0$, $p=0.003$), indistinct, brown supratympanic line (versus distinct black supratypmanic line in *L. applebyi*) and tuberculate skin texture (versus mostly smooth in *L. melicus*). *L. pallidus* **sp. nov**. differs from *L. pyrrhops* by having a significantly smaller and non-overlapping male body size (Wilcoxon post-hoc $Z=3.2$, $p=0.002$), smaller relative diameter of the eye (Wilcoxon post-hoc $Z=3.2$, $p=0.002$), indistinct, brown supratympanic line (versus distinct black supratypmanic line in *L. pyrrhops*) and tuberculate skin texture (versus only slightly shagreened in *L. pyrrhops*). *L. pallidus* **sp. nov**. differs from *L. ardens* **sp. nov.** by having a significantly larger body size (Wilcoxon post-hoc $Z=-3.8$, $p<0.001$), larger relative tympanum diameter (Wilcoxon post-hoc $Z=-2.7$, $p=0.007$), indistinct, brown supratympanic line (versus distinct black supratypmanic line in *L. ardens* **sp. nov**) and tuberculate skin texture (versus mostly smooth in *L. ardens* **sp. nov**). *L. pallidus* **sp. nov**. differs from *L. kalonensis* **sp. nov.** by having a significantly smaller body size (Wilcoxon post-hoc $Z=3.0$, $p=0.002$), larger relative tympanum diameter (Wilcoxon post-hoc $Z=-3.1$, $p=0.002$), indistinct, brown supratympanic line (versus distinct black supratypmanic line in most *L. kalonensis* **sp. nov**) and tuberculate skin texture (versus mostly smooth in *L. kalonensis* **sp. nov**). *L. pallidus* **sp. nov**. differs from *L. maculosus* **sp. nov.** by having indistinct, brown supratympanic line (versus distinct black supratypmanic line in *L. maculosus* **sp. nov**) and tuberculate skin texture (versus mostly smooth in *L.*

maculosus **sp. nov**). *L. pallidus* **sp. nov**. differs from *L. tadungensis* **sp. nov.** by having a significantly larger relative tibia length (Wilcoxon post-hoc Z=-3.1, p=0.002), larger relative distance between the eye and tympanum (Wilcoxon post-hoc Z=-2.4, p=0.019), indistinct, brown supratympanic line (versus distinct black supratympanic line in *L. maculosus* **sp. nov**) and tuberculate skin texture (versus mostly smooth in *L. maculosus* **sp. nov**). See Table 4 and Fig. 4.

The male advertisement call of *L. pallidus* **sp. nov.** differs from all members of the *L. applebyi* group. The call of *L. pallidus* **sp. nov.** differs from *L. applebyi* in call duration, having a relatively long, pulsed introductory note, having one pulse in non-introductory notes, and by average note repetition rate and average dominant frequency. *L. pallidus* **sp. nov.** differs from *L. bidoupensis* in call duration, in having a distinct, pulsed introductory note, and by average note repetition rate and perhaps average dominant frequency (non-overlapping but similar values); from *L. melicus* in call duration, number of pulses in the introductory note, average note repetition rate and average dominant frequency; from *L. pyrrhops* in call duration, average number of pulses in introductory note, average note repetition rate and potentially by dominant frequency; from *L. ardens* **sp. nov.** differs by call duration, number of pulses in the introductory note, note repetition rate and dominant frequency; from *L. kalonensis* **sp. nov.** in average call duration, average number of pulses in the introductory note and average note repetition rate; from *L. maculosus* **sp. nov.** in average call duration number of notes per call, and having a distinct introductory note; from *L. tadungensis* **sp. nov.** in average call duration, average duration of introductory note, and note repetition rate. See Table 7 and Figs. 5–6.

Leptolalax pallidus **sp. nov.** differs from all species within the *L. applebyi* group by >4.7% divergence at the 16S gene fragment examined. Interspecific variation in three *L. pallidus* **sp. nov.** collected from <200 m apart was 0%.

***Leptolalax kalonensis* sp. nov.**
Figs. 8B, 9B, 11.

Holotype. IEBR A.2014.15, adult male, collected from rocky crevice, 0.5 m from 4–5 m wide, rocky stream in disturbed evergreen forest in Song Luy Watershed Forest, Binh Thuan Province, Vietnam (11.2748º N, 108.2109º E; 200 m elevation; Figs 1, 9F). Collected 5 August 2011 by Dao T. A. Tran, David Kizirian, Truong Q. Nguyen, Pedro L. V. Peloso, and Cuong T. Pham.

Paratypes. AMNH A191768–9, 2 adult males, and IEBR A.2014.22, one adult female, collected on 6 August 2011; AMNH A191770, adult male collected on 11 August 2011; AMNH A191761 adult male collected on 12 August 2011; IEBR A.2014.18, adult male collected on 13 August 2011; all from disturbed evergreen forest in Song Luy Watershed Forest, Binh Thuan Province, Vietnam (11.2748º N, 108.2109º E; 200 m elevation). AMNH A191762, AMNH A191765, AMNH A191763, IEBR A.2014.19, AMNH A191764, IEBR A.2014.21, AMNH A191767, seven adult males, and AMNH A191766, IEBR A.2014.20, two adult females, collected on 5 August 2011; IEBR A.2014.15, adult male, collected on 12 August 2011; IEBR A.2014.16 and IEBR A.2014.17, two adult males, collected on 13 August 2011 in disturbed evergreen forest in Song Luy Watershed Forest, Binh Thuan Province, Vietnam (11.2919º N, 108.2150º E, 571 m elevation). Paratypes were collected by Dao T. A. Tran, David Kizirian, Truong Q. Nguyen, Pedro L. V. Peloso, and Cuong T. Pham.

Etymology. Specific epithet "*kalonensis*" is in reference to the type locality of the species, which is in close proximity to the village previously known as Kalon.

Diagnosis. Assigned to the genus *Leptolalax* on the basis of the following characters: small size, rounded finger tips, the presence of an elevated inner palmar tubercle not continuous to the thumb, presence of macroglands on body (including supra–axillary, pectoral, femoral and ventrolateral glands), the absence of vomerine teeth, the presence of tubercles on eyelids, and anterior tip of snout with pale vertical bar (Dubois 1983; Lathrop *et al*. 1998; Delorme *et al*. 2006). *Leptolalax kalonensis* **sp. nov.** is distinguished from its congeners by a combination of (1) supra–axillary and ventrolateral glands present; (2) pale brownish pink ventral surface with white speckling; (3) small/medium SVL for the genus (25.8–30.6 mm in 16 adult males, 28.9–30.6 mm in three females); (4) toes lacking webbing and lateral fringes; (5) tibia length 45–52% of SVL in males; (6) pectoral gland 2.5–7.0% of SVL in males, (7) mostly smooth dorsum, (8) iris gold, coppery orange in upper third in some specimens (9) distinct black supratympanic line present in most specimens, (10) an advertisement call with 4–5 notes including introductory note, comprising almost one-third of each call duration.

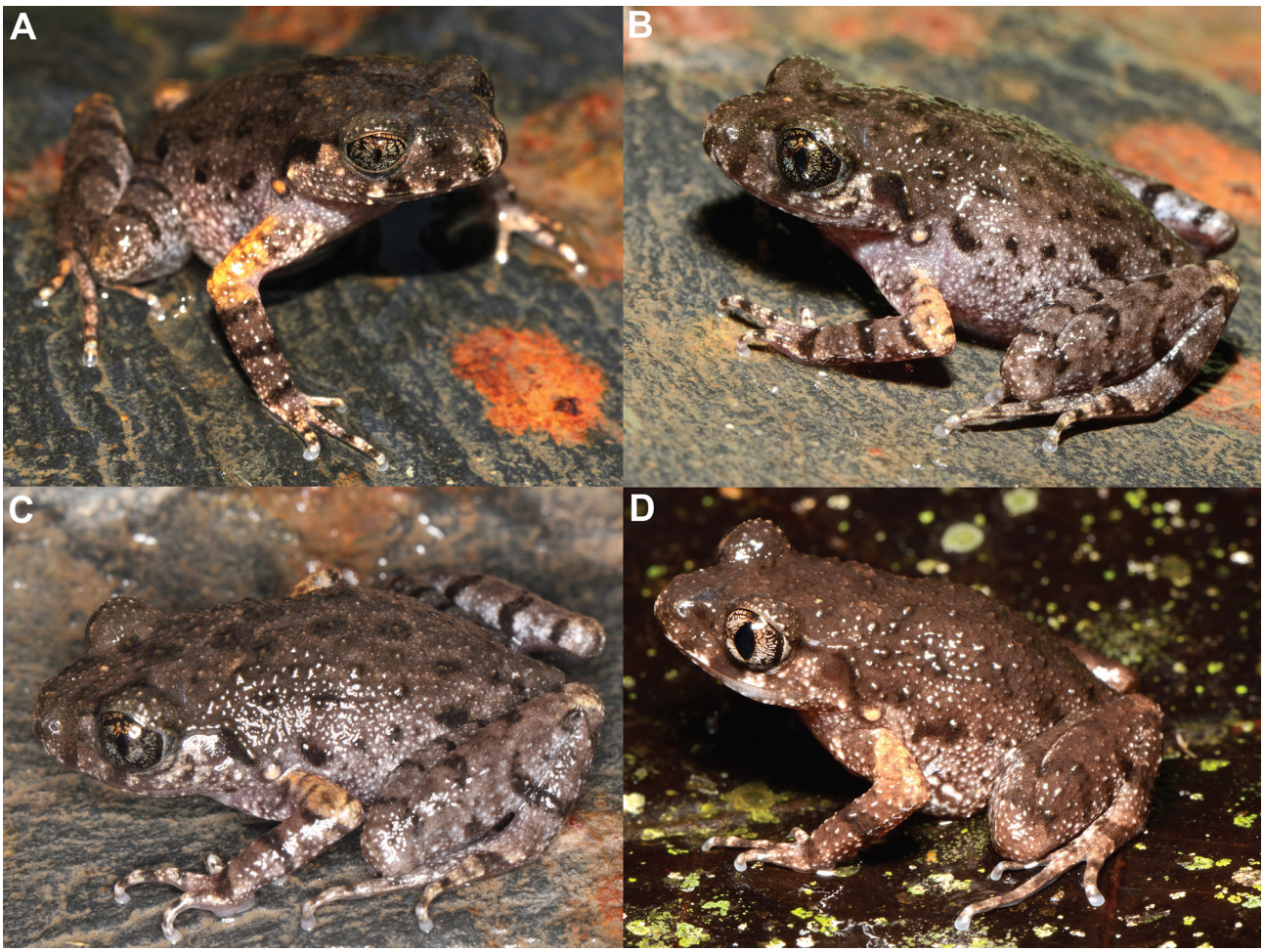

FIGURE 12. *Leptolalax kalonensis* **sp. nov**. in life (A) male holotype IEBR A.2014.15, (B) male paratype AMNH A191770, (C) male paratype AMNH A191770, (D) paratype (registration number not recorded).

Description of holotype. Head width slightly subequal to head length; snout slightly truncate in dorsal view and in profile, projecting slightly beyond margin of the lower jaw; nostril closer to snout than eye; canthus rostralis indistinct, gently rounded; lores sloping; pupil vertical; eye diameter smaller than snout length; tympanum indistinct, round, diameter smaller than that of the eye; tympanic rim slightly elevated relative to skin of temporal region; vomerine teeth absent; pineal ocellus absent; vocal sac openings slit–like, located posteriolaterally on floor of mouth; tongue wide with broad, shallow notch at posterior tip; supratympanic ridge distinct, running from eye to axillary gland. Tips of fingers rounded, very slightly swollen; relative finger lengths I < IV = II < III; nuptial pad absent; subarticular tubercles absent; a large, round inner palmar tubercle distinctly separated from small, laterally compressed outer palmar tubercle; finger webbing and dermal fringes absent. Tips of toes like fingers; relative toe length I < II < V < III < IV; subarticular tubercles absent, replaced by dermal ridges, distinct on base of toes II and III; large, oval inner metatarsal tubercle present, outer metatarsal tubercle absent; toe webbing rudimentary; lateral fringes absent. Tibia 46% of snout–vent length; tibiotarsal articulation reaching to anterior edge of eye. Skin on dorsum smooth; ventral skin smooth; pectoral gland oval, 1.0 mm diameter; femoral gland oval, 1.1 mm diameter, on posteroventral surface of thigh, closer to knee than to vent; supra–axillary gland oval, raised, 1.2 mm diameter. Ventrolateral glands indistinctly present as broken lines.

Colour of holotype in life. Dorsal surface brown with slightly darker interorbital bar; faint dark W-shaped marking between axilla (Fig. 12A). Darker brown line along supratympanic ridge, terminating above axilla, encompassing most of tympanum; transverse dark brown bars on dorsal surface of thighs, tibia, tarsus, lower arms, fingers and toes; elbows and upper arms paler brown; several small dark brown spots on sides from groin to axilla. Dark brownish ventral surface with white speckling on ventral surfaces of throat, chest and belly, more sparse on legs and arms. Supra-axillary gland copper; femoral glands white; pectoral glands white, ventrolateral glands white. Iris copper in upper half, gold in lower half, black reticulations throughout.

Colour of holotype in preservative. Dorsum greyish brown with darker brown, elongated, oval blotches and intraorbital blotch; dark brown/black banding on dorsal surface of tibiotarsus, antebrachium, hands and feet. Groin on blotch (Fig. 8B). Ventral surface cream. Macroglands creamy white.

Measurements (mm). Holotype: SVL 27.5, HDL 10.2, HDW 10.1, SNT 4.3, EYE 3.6, IOD 2.9, TMP 1.7, TEY 1.3, TIB 12.6, EN 2.5, IN 2.8, NS 1.6, ML 6.7, PL 11.5.

Variation. Measurements of the type series are shown in Tables 2–3 and representative photographs of paratypes are shown in Figs. 9B and 12. AMNH A191768, AMNH A191769, IEBR A.2014.16, IEBR A.2014.17, and IEBR A.2014.22 are darker in dorsal colouration and have less distinct patterning. IEBR A.2014.18 and AMNH A191763 are pale and have only dark brown, rather than black markings. Specimens vary in degree of patterning on dorsum. Specimens vary in degree of medium brown speckling on venter; AMNH A191768, IEBR A.2014.16, AMNH A191762, IEBR A.2014.20, and AMNH A191766 have variably medium brown throats with white speckling and medium brown speckling on chest and belly (especially IEBR A.2014.16). The ventrolateral line varies in distinctness and completeness; the most distinct and complete in AMNH A191769.

Advertisement call. Call descriptions are based on the call of AMNH A191770, recorded at 26.4 ºC ambient temperature. Calls were an average of 201 ms in duration and consisted of 4–5 notes (Table 7, Fig. 6B). Introductory notes of low relative amplitude were present in all calls, were an average of 29% of the call duration, and contained up to an average of 15 pulses. Non-introductory notes near-invariably contained a single pulse. Notes were repeated an average of 16 notes/s. The average dominant frequency was 2.8 kHz, spread more widely (2.6–2.9 kHz) in non-introductory notes. Harmonics and a fundamental frequency were not visible due to poor recording quality. To the human ear, the advertisement call of *L. kalonensis* **sp. nov.** is a short rasp, similar to an orthopteran.

Ecology. All specimens of *Leptolalax kalonensis* **sp. nov.** were found in evergreen forest between 200–791 m elevation in Song Luy Watershed Forest. Specimens were located on the ground, 0.5–4.0 m from 2–5 m wide, shallow, rocky streams (Fig. 9F). Forest in the area was disturbed secondary forest, consisting of discontinuous patches of small hardwoods, bamboo and shrubs. Forest on mountain slopes was replaced by plantations and cultivated fields.

Distribution. *Leptolalax kalonensis* **sp. nov.** is only known from Song Luy Watershed Forest in Binh Thuan Province, Vietnam. The greatest distance between known localities for the species is 43 km. Given the relatively large distance between localities, low elevation, and relatively larger streams, this species is likely to be more widely distributed than other species in the *L. applebyi* group.

Comparisons. *Leptolalax kalonensis* **sp. nov.** differs from all other *Leptolalax* species in mainland Southeast Asia on the basis of morphology, and from all congeners in the region for which comparable data is available on the basis of molecular and acoustic data.

The new species differs from *L. aereus* by ventral coloration and presence of black supratympanic line, from *L. bourreti* by ventral coloration, from *L. botsfordi* by ventral coloration, from *L. croceus* by ventral coloration, presence of black supratympanic line, and skin texture; from *L. eos* by ventral coloration, male body size, presence of black supratympanic line, and lateral fringes on toes; from *L. firthi* by ventral coloration, presence of black supratympanic line, skin texture and lateral fringes on toes; from *L. fuliginosus* by ventral coloration and iris coloration; from *L. heteropus* by ventral coloration and male body size; from *L. kecil* by ventral coloration, male body size and iris coloration; from *L. melanoleucus* by ventral coloration and iris coloration; from *L. minimus* by ventral coloration; from *L. nahangensis* by ventral coloration and male body size; from *L. nyx* by ventral coloration, from *L pelodytoides* by ventral coloration; from *L. platycephalus* by ventral coloration and male body size; from *L. pluvialis* by ventral coloration and male body size; from *L. solus* by ventral coloration and iris coloration; from *L. sungi* by ventral coloration, male body size and iris coloration; from *L. tuberosus* by ventral coloration, iris coloration and skin texture; from *L. ventripunctatus* by ventral coloration and iris coloration; and from *L. zhangyangpingi* by ventral coloration, male body size and iris coloration. See Table 8 for details.

From members of the *L. applebyi* group, *L. kalonensis* **sp. nov**. differs from all species by at least one morphological character (all following morphometric differences refer to males only). The new species differs from *L. applebyi* by having a significantly larger body size (Wilcoxon post-hoc $Z=4.0$, $p<0.001$), larger relative tibia length (Wilcoxon post-hoc $Z=2.8$, $p=0.005$), greater relative diameter of the eye (Wilcoxon post-hoc $Z=2.9$, $p=0.004$), and larger relative pectoral gland size (Wilcoxon post-hoc $Z=2.6$, $p=0.009$). *L. kalonensis* **sp. nov**. differs from *L. bidoupensis* by having a significantly larger body size (Wilcoxon post-hoc $Z=4.4$, $p<0.001$), larger relative

tibia length (Wilcoxon post-hoc Z=3.2, p=0.001), larger relative eye size (Wilcoxon post-hoc Z=2.3, p=0.019), and gold iris (versus reddish upper and silver below). *L. kalonensis* **sp. nov**. differs from *L. melicus* by having a significantly larger body size (Wilcoxon post-hoc Z= -3.9, p<0.001), and greater length between eye and tympanum (Wilcoxon post-hoc Z= -3.0, p=0.003). *L. kalonensis* **sp. nov**. differs from *L. pyrrhops* by having a significantly smaller body size (Wilcoxon post-hoc Z=3.7, p<0.001), smaller relative tympanum size (Wilcoxon post-hoc Z=2.7, p=0.006), smaller relative distance between eye and tympanum (Wilcoxon post-hoc Z=2.2, p=0.025) and smaller relative eye width (Wilcoxon post-hoc Z=3.5, p=0.001). *L. kalonensis* **sp. nov**. differs from *L. ardens* **sp. nov.** by having a significantly greater body size (Wilcoxon post-hoc Z=4.7, p<0.001). *L. kalonensis* **sp. nov**. differs from *L. pallidus* **sp. nov.** by having a significantly greater body size (Wilcoxon post-hoc Z=3.0, p=0.002), smaller relative tympanum diameter (Wilcoxon post-hoc Z= -3.1, p=0.002), black supratympanic line in most specimens (versus no black supratypmanic line in *L. pallidus* **sp. nov**) and smooth skin texture (versus tuberculate in *L. kalonensis* **sp. nov**). *L. kalonensis* **sp. nov**. differs from *L. maculosus* **sp. nov.** by having a significantly greater body size (Wilcoxon post-hoc Z= -2.7, p=0.007). *L. kalonensis* **sp. nov**. differs from *L. tadungensis* **sp. nov.** by having a significantly greater body size (Wilcoxon post-hoc Z= -3.3, p=0.001), and greater relative tibia length (Wilcoxon post-hoc Z=-3.5, p=0.001). See Table 4 and Fig. 4.

Although based on a single call recording, the male advertisement call of *L. kalonensis* **sp. nov.** differs from all members of the *L. applebyi* group with the exception of *L. ardens* **sp. nov.** In particular, the species differs from *L. applebyi* in length of introductory note and dominant frequency; from *L. bidoupensis* in call duration, presence of a distinct introductory note and dominant frequency (although similar); from *L. melicus* in dominant frequency; from *L. pyrrhops* by dominant frequency; from *L. pallidus* **sp. nov.** by average call duration, average number of pulses in the introductory note and average note repetition rate; from *L. maculosus* **sp. nov.** by average call duration, number of notes per call, and having a distinct introductory note; from *L. tadungensis* **sp. nov.** by average call duration, and average duration of introductory note. See Table 7 and Figs. 5–6.

Leptolalax kalonensis **sp. nov.** differs from all species within the *L. applebyi* group by >5.2% divergence at the 16S gene fragment examined. Interspecific variation in four *L. kalonensis* **sp. nov.** collected from up to 43 km apart was 0.0–0.6%.

***Leptolalax maculosus* sp. nov.**
Figs. 8C, 9C, 13.

Holotype. UNS00513, adult male, in dry stream bed in evergreen forest in Phuoc Binh National Park, Ninh Thuan Province, Vietnam (12.0152º N, 108.7271º E, 900 m elevation, Fig. 1). Collected on 24 September 2011 by Dao T. A. Tran and Duong T. T. Le.

Paratypes. ZFMK 96600, adult male from same date and location as holotype. AMS R 177660, adult male, and UNS00514, adult female, collected on 27 September 2011 from evergreen forest in Phuoc Binh National Park, Ninh Thuan Province, Vietnam (12.0413º N, 108.7385º E, 1166 m elevation). All specimens were collected by Dao T. A. Tran and Duong T. T. Le.

Etymology. The specific name "*maculosus*", meaning spotted, speckled, mottled or variegated, is used as an adjective in reference to the more mottled dorsal pattern of this species.

Diagnosis. Assigned to the genus *Leptolalax* on the basis of the following characters: small size, rounded finger tips, the presence of an elevated inner palmar tubercle not continuous to the thumb, presence of macroglands on body (including supra–axillary, pectoral, femoral and ventrolateral glands), the absence of vomerine teeth, the presence of tubercles on eyelids, and anterior tip of snout with pale vertical bar (Dubois 1983; Lathrop *et al*. 1998; Delorme *et al*. 2006). *Leptolalax maculosus* **sp. nov.** is distinguished from its congeners by a combination of (1) supra-axillary and ventrolateral glands present; (2) dark brownish red ventral surface with white speckling; (3) small/medium SVL for the genus (24.2–26.6 mm in three adult males, 27.0 mm in one female); (4) toes lacking webbing and lateral fringes; (5) tibia length 48–50% of SVL in males; (6) pectoral gland 3.5–4.2% of SVL in males, (7) mostly smooth dorsum, (8) iris copper in upper half and gold in lower half (9) distinct black supratympanic line present, (10) an advertisement call with 7–38 notes, lacking a distinct introductory note.

FIGURE 13. *Leptolalax maculosus* **sp. nov**. in life (A) dorsolateral view of male holotype UNS 00513, (B) anteroventral view of male holotype UNS 00513, (C) male holotype AMS R 177660, (D) female paratype UNS 00514.

Description of holotype. Head width equal to head length; snout rounded in dorsal view and slightly truncate in profile, projecting slightly beyond margin of the lower jaw; nostril closer to snout than to eye; canthus rostralis indistinct, gently rounded; lores straight; pupil vertical; eye diameter slightly larger than snout length; tympanum distinct, round, diameter smaller than that of the eye; tympanic rim slightly elevated relative to skin of temporal region; vomerine teeth absent; pineal ocellus absent; vocal sac openings slit–like, located posteriolaterally on floor of mouth; tongue wide with broad, shallow notch at posterior tip; supratympanic ridge distinct, running from eye to axillary gland. Tips of fingers rounded, very slightly swollen; relative finger lengths I < IV = II < III; nuptial pad absent; subarticular tubercles absent; a large, round inner palmar tubercle distinctly separated from smaller, laterally compressed outer palmar tubercle; finger webbing and dermal fringes absent. Tips of toes like fingers; relative toe length I < II < V < III < IV; subarticular tubercles absent; large, oval inner metatarsal tubercle present, outer metatarsal tubercle absent; toe webbing rudimentary, most visible between toes II and III; slight lateral fringes present. Tibia 48% of snout–vent length; tibiotarsal articulation reaching tip of snout. Skin on dorsum smooth; ventral skin smooth; pectoral gland oval, 1.0 mm diameter; femoral gland oval, approximately 1.7 mm diameter, on posteroventral surface of thigh, slightly closer to knee than to vent; supra–axillary gland oval, raised, 1.3 mm diameter. Ventrolateral glands forming broken lines.

Colour of holotype in life. Dorsal surface dark brown with irregular, darker brown blotch down back; small, pale brown blotches scattered over dorsum; dark interorbital bar with pale copper edging anteriorly; two small, pale copper V-markings between axilla (Fig. 13A, B). Black line along supratympanic ridge, terminating above axilla,

encompassing most of tympanum; irregular copper band under black supratympanic line; transverse dark brown bars on dorsal surface of thighs, tibia, tarsus, lower arms, fingers and toes; elbows and upper arms copper; numerous, small darker brown spots on sides from groin to axilla. Brownish pink ventral surface with white speckling on ventral surfaces of throat, chest, belly, legs and arms. Supra-axillary gland copper; femoral glands white; pectoral glands white, ventrolateral glands white. Iris copper in upper half, gold in lower half, black reticulations throughout.

Colour of holotype in preservative. Dorsum medium brown with small, pale brown blotches on top of head, barely visible paler intraorbital blotch; dark brown/black banding on dorsal surface of tibiotarsus, antebrachium, hands and feet (Fig. 8C). Black blotch on groin. Ventral surface medium brown with white speckling. Macroglands creamy white.

Measurements (mm). Holotype: SVL 24.2, HDL 8.9, HDW 9.0, SNT 3.3, EYE 3.4, IOD 3.5, TMP 1.5, TEY 0.9, TIB 11.6, EN 2.3, IN 2.3, NS 1.1, ML 6.0, PL 10.1.

Variation: Measurements of the type series are shown in Tables 5–6 and representative photographs of paratypes are shown in Figs. 9C and 15. AMS R 177660 and to a lesser extent ZFMK 96600 have more distinct patterning, with paler blotches on the dorsum

Advertisement call. Call descriptions are based on the calls of two individuals, recorded at 23.3–24.1 ºC ambient temperature. Calls were an average of 907 ms in duration and consisted of 7–38 notes (Table 7, Fig. 6C). Calls were highly amplitude modulated, with a slow rise in amplitude, and amplitude peaking towards the middle of each note. Notes near-invariably contained a single pulse. Notes were repeated an average of 17 notes/s, but note repetition rate was higher at the start of each call. The average dominant frequency was 2.7 kHz, with peak frequency spread over ~2.7–3.5 kHz. A fundamental frequency was not visible. To the human ear, the advertisement call of *L. maculosus* **sp. nov**. is a squealch grading gently into a chirp.

Ecology. All specimens of *Leptolalax maculosus* **sp. nov.** were found in evergreen forest between 900–1166 m elevation at Phuoc Binh National Park. Specimens were found within leaf-litter and in clay holes in a dry stream bed of 1.5–2.0 m width, connecting to a larger stream.

Distribution. *Leptolalax maculosus* **sp. nov.** is only known from Phuoc Binh National Park, Ninh Thuan Province, Vietnam. The maximum distance between known localities is only 3.2 km.

Comparisons. *Leptolalax maculosus* **sp. nov.** differs from all other *Leptolalax* species in mainland Southeast Asia on the basis of morphology, and from all congeners in the region for which comparable data is available on the basis of molecular and acoustic data.

The new species differs from *L. aereus* by ventral coloration and presence of distinct black supratympanic line, from *L. bourreti* by ventral coloration and male body size, from *L. botsfordi* by male body size and relative body weight (0.41–0.47 versus 0.75–0.94 g/mm in *L. botsfordi*), from *L. croceus* by ventral coloration, presence of black supratympanic line and iris coloration; from *L. eos* by ventral coloration, male body size, presence of black supratympanic line and lateral fringes on toes; from *L. firthi* by ventral coloration, iris coloration and lateral fringes on toes; from *L. fuliginosus* by ventral coloration, male body size and iris coloration; from *L. heteropus* by ventral coloration and iris coloration; from *L. kecil* by ventral coloration, male body size and iris coloration; from *L. melanoleucus* by ventral coloration and iris coloration; from *L. minimus* by ventral coloration; from *L. nahangensis* by ventral coloration and male body size; from *L. nyx* by ventral coloration and male body size, from *L pelodytoides* by ventral coloration and male body size; from *L. platycephalus* by ventral coloration and male body size; from *L. pluvialis* by ventral coloration and male body size; from *L. solus* by ventral coloration, male body size and iris coloration; from *L. sungi* by ventral coloration, male body size and iris coloration; from *L. tuberosus* by ventral coloration, presence of black supratympanic line and skin texture; from *L. ventripunctatus* by ventral coloration and iris coloration; and from *L. zhangyangpingi* by ventral coloration, male body size and iris coloration. See Table 8 for details.

From members of the *L. applebyi* group, *L. maculosus* **sp. nov**. differs from all species by at least one morphological character (all following morphometric differences refer to males only). The new species differs from *L. applebyi* by having a significantly greater body size (Wilcoxon post-hoc Z=2.7, p=0.007), greater relative head width (Wilcoxon post-hoc Z=2.7, p=0.007), greater relative diameter of the eye (Wilcoxon post-hoc Z=2.2, p=0.025), and greater relative pectoral gland size (Wilcoxon post-hoc Z=2.4, p=0.017). *L. maculosus* **sp. nov**. differs from *L. bidoupensis* by having a significantly greater relative tibia length (Wilcoxon post-hoc Z=2.4, p=0.018), and a bronze iris (versus reddish upper and silver below in *L. bidoupensis*). *L. maculosus* **sp. nov**. differs

from *L. melicus* by having a significantly greater body size (Wilcoxon post-hoc Z=2.6, p=0.009), and greater length between eye and tympanum (Wilcoxon post-hoc Z=2.1, p=0.034). *L. maculosus* **sp. nov**. differs from *L. pyrrhops* by having a significantly smaller body size (Wilcoxon post-hoc Z= -2.6, p=0.010), smaller relative length between eye and tympanum (Wilcoxon post-hoc Z= -2.4, p=0.018) and smaller relative diameter of the eye (Wilcoxon post-hoc Z=-2.4, p=0.018). *L. maculosus* **sp. nov**. differs from *L. ardens* **sp. nov.** by having a significantly greater body size (Wilcoxon post-hoc Z=2.8, p=0.006). *L. maculosus* **sp. nov**. differs from *L. pallidus* **sp. nov.** by having a black supratympanic line (versus no black supratypmanic line in *L. pallidus* **sp. nov**) and smooth- finely shagreened skin texture (versus tuberculate in *L. pallidus* **sp. nov**). *L. maculosus* **sp. nov**. differs from *L. kalonensis* **sp. nov.** by having a significantly smaller body size (Wilcoxon post-hoc Z=-2.7, p=0.007). *L. maculosus* **sp. nov**. differs from *L. tadungensis* **sp. nov.** by having a significantly greater relative tibia length (Wilcoxon post-hoc Z=-2.5, p=0.013). See Table 4 and Fig. 5.

The male advertisement call of *L. maculosus* **sp. nov.** differs from all species in the *L. applebyi* group. The call of the new species differs from *L. applebyi* in call duration, number of notes per call, an introductory note, and dominant frequency; from *L. bidoupensis* in call duration, average number of notes per call, presence of an introductory note, and average dominant frequency; from *L. melicus* in call duration, number of notes per call, having an indistinct introductory note, and dominant frequency; from *L. pyrrhops* by call duration, number of notes per call, having an indistinct introductory note, and dominant frequency; from *L. ardens* **sp. nov.** by call duration, number of notes per call and dominant frequency; from *L. pallidus* **sp. nov.** by call duration and number of notes per call; from *L. kalonensis* **sp. nov.** by average call duration, and number of notes per call; from *L. tadungensis* **sp. nov.** by call duration, number of notes per call, having a less distinct introductory note and different relative duration of introductory note. See Table 7 and Figs. 5–6.

Leptolalax maculosus **sp. nov.** differs from all species within the *L. applebyi* group by >6.3% divergence at the 16S gene fragment examined. Interspecific variation in four *L. maculosus* **sp. nov.** collected from up to ~3 km apart was 0.0–0.2%.

***Leptolalax tadungensis* sp. nov.**
Figs. 8D, 14.

Holotype. UNS00516, adult male, in dry stream in evergreen forest in Ta Dung Nature Reserve, Dak Nong Province, Vietnam (11.8350º N, 108.0081º E, 1262 m elevation, Fig. 1, 9G). Collected on 13 July 2010 by Dao T. A. Tran, Vinh Q. Dau, and Huy D. Hoang.

Paratypes. AMS R 177666 and ZFMK 96601, two adult males, collected on same date and locality as holotype. UNS00515, AMS R 177661, AMS R 177662, ZFMK 96602 and ZFMK 96603, five adult males collected on 17 July 2010 in Ta Dung Nature Reserve, Dak Nong Province, Vietnam (11.8388º N, 107.8945º E, 720 m elevation). UNS 00526 and UNS 00527, two adult males, collected on 17 July 2011 in Ta Dung Nature Reserve, Dak Nong Province, Vietnam (11.8561º N, 108.0371º E, 1932 m elevation); UNS 00517 adult female, collected at same site on 16 July 2011. Specimens were collected by Dao T. A. Tran and Huy D. Hoang.

Etymology. Specific epithet "*tadungensis*" is in reference to the type locality of the species, Ta Dung Nature Reserve.

Diagnosis. Assigned to the genus *Leptolalax* on the basis of the following characters: small size, rounded finger tips, the presence of an elevated inner palmar tubercle not continuous to the thumb, presence of macroglands on body (including supra–axillary, pectoral, femoral and ventrolateral glands), the absence of vomerine teeth, the presence of tubercles on eyelids, and anterior tip of snout with pale vertical bar (Dubois 1983; Lathrop *et al*. 1998; Delorme *et al*. 2006). *Leptolalax tadungensis* **sp. nov.** is distinguished from its congeners by a combination of (1) supra–axillary and ventrolateral glands present; (2) dark brownish red ventral surface with white speckling; (3) small/medium SVL for the genus (23.5–26.0 mm in eight adult males, 32.1 mm in one female); (4) toes lacking webbing and lateral fringes; (5) tibia length 43–48% of SVL in males; (6) pectoral gland 3.3–5.4% of SVL in males, (7) smooth dorsum, (8) iris dark gold, (9) distinct black supratympanic line present, (10) an advertisement call with 4–7 notes with the first, introductory note encompassing less than a tenth of each call.

Description of holotype. Head width less than head length; snout rounded in dorsal view and slightly truncate in profile, projecting slightly beyond margin of the lower jaw; nostril closer to snout than eye; canthus rostralis

indistinct, gently rounded; lores straight; vertical pupil; eye diameter smaller than snout length; tympanum distinct, round, diameter smaller than that of the eye; tympanic rim slightly elevated relative to skin of temporal region; vomerine teeth absent; pineal ocellus absent; vocal sac openings slit–like, located posteriolaterally on floor of mouth; tongue wide with broad, shallow notch at posterior tip; supratympanic ridge distinct, running from eye to axillary gland. Tips of fingers rounded, very slightly swollen; relative finger lengths I < IV = II < III; nuptial pad absent; subarticular tubercles absent; a large, round inner palmar tubercle separated from a much smaller, laterally compressed outer palmar tubercle; finger webbing and dermal fringes absent. Tips of toes like fingers; relative toe length I < II < V < III < IV; subarticular tubercles absent; large, oval inner metatarsal tubercle present, outer metatarsal tubercle absent; toe webbing rudimentary, slight lateral fringes present. Tibia 47% of snout–vent length; tibiotarsal articulation reaches snout. Skin on dorsum smooth; ventral skin smooth; pectoral gland oval, 1.0 mm diameter; femoral gland small, oval, approximately 0.6 mm diameter, on posteroventral surface of thigh, closer to knee than to vent; supra–axillary gland oval, raised, 1.0 mm diameter. Ventrolateral glands indistinct.

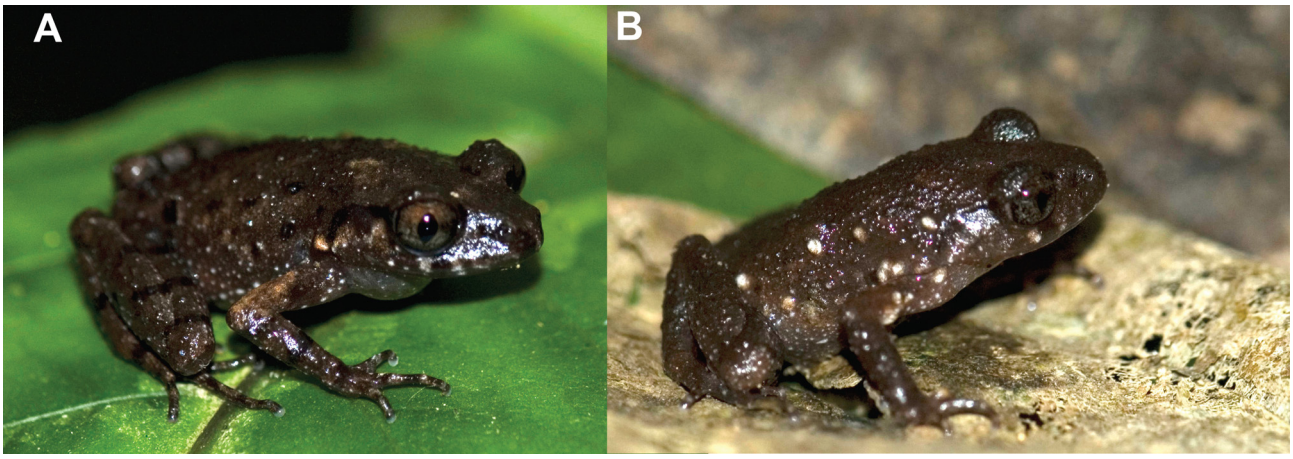

FIGURE 14. *Leptolalax tadungensis* **sp. nov**. in life (A) topotypic male (B) male paratype UNS 00515 (note the black supratympanic fold and upper tympanum).

Colour of holotype in life. Dorsal surface dark brown; very faint transverse darker brown bars on the dorsal surface of the thighs, tibia, tarsus, lower arms, fingers and toes. Black line along supratympanic ridge, terminating above axilla, encompassing posterodorsal half of tympanum; anteroventral half paler brown; transverse dark brown bars on dorsal surface of thighs, tibia, tarsus, lower arms, fingers and toes; elbows and upper arms slightly paler, brownish copper; numerous, small darker brown spots on sides from groin to axilla. Dark brown ventral surface with fine white speckling on ventral surfaces of throat, chest, belly, legs and arms; most dense on chest. Supra-axillary gland copper; femoral glands white; pectoral glands white. Iris copper, fine black reticulations throughout.

Colour of holotype in preservative. Dorsum uniform dark brown with scattered small black blotches on flanks and larger black spot on groin; fine black banding on dorsal surface of tibiotarsus, antebrachium, hands and feet (Fig. 8D). Ventral surface medium brown with only very faintly visible, fine white speckling. Macroglands white.

Measurements (mm). Holotype: SVL 24.9, HDL 9.4, HDW 8.9, SNT 3.8, EYE 2.9, IOD 3.4, TMP 1.6, TEY 0.9, TIB 11.7, EN 2.2, IN 2.2, NS 1.7, ML 6.0, PL 10.4.

Variation. Measurements of the type series are shown in Tables 5–6 and representative photographs of paratypes are shown in Fig. 14. Little variation in dorsal colouration. Single female specimen UNS 00527 is paler in colour with a more truncate snout. The white speckling on venter is more distinct in UNS 00527, UNS00517, and AMS R 177661, forming small blotches in UNS 00527, and UNS00517; the dorsolateral line is more distinct and less broken in these specimens. UNS 00526 and UNS00517 have a slightly shagreened skin texture in preservative, possibly an artefact of preservation (with these specimens being better preserved).

Advertisement call. Call descriptions are based on the calls of four individuals, recorded at 12.9–22.3ºC ambient temperature. Calls were an average of 291 ms in duration and consisted of 4–7 notes (Table 7, Figure 6D). Introductory notes were very short and quite similar to non-introductory notes, comprising only 3–9% of the call duration, and were indistinctly pulsed. Non-introductory notes contained 1–4 pulses. Notes were repeated an

average of 14.3 notes/s. The average dominant frequency was 2.8 kHz. Harmonics were weakly present at ~6.3, 13.2, 16.6 kHz, and a fundamental frequency was not visible. To the human ear, the advertisement call of *L. pallidus* **sp. nov.** is a short raspy chirp, similar to an orthopteran.

Ecology. All specimens of *Leptolalax tadungensis* **sp. nov.** were found in evergreen forest in Ta Dung Nature Reserve between 720–1932 m elevation (Fig. 9H). All frogs were found calling during rainy conditions. Frogs collected at the type locality were in underground rocky crevices. Individuals collected on Ta Dung Mountain (~1930 m elevation) were calling from the ground or under leaf litter.

Distribution. *Leptolalax tadungensis* **sp. nov.** is only known from Ta Dung Nature Reserve, Dak Nong Province, Vietnam. The greatest distance between known localities for the species is 15.7 km.

Comparisons. *Leptolalax tadungensis* **sp. nov.** differs from all other *Leptolalax* species in mainland Southeast Asia on the basis of morphology, and from all congeners in the region for which comparable data is available on the basis of molecular and acoustic data.

The new species differs from *L. aereus* by ventral coloration and presence of distinct black supratympanic line, from *L. bourreti* by ventral coloration, from *L. botsfordi* by male body size, from *L. croceus* by ventral coloration, presence of black supratympanic line, iris coloration and skin texture; from *L. eos* by ventral coloration, male body size, presence of black supratympanic line and lateral fringes on toes; from *L. firthi* by ventral coloration, iris coloration, skin texture and lateral fringes on toes; from *L. fuliginosus* by ventral coloration and iris coloration; from *L. heteropus* by ventral coloration and iris coloration; from *L. kecil* by ventral coloration, male body size and iris coloration; from *L. melanoleucus* by ventral coloration and iris coloration; from *L. minimus* by ventral coloration; from *L. nahangensis* by ventral coloration and male body size; from *L. nyx* by ventral coloration; from *L pelodytoides* by ventral coloration; from *L. platycephalus* by ventral coloration and male body size; from *L. pluvialis* by ventral coloration and male body size; from *L. solus* by ventral coloration and iris coloration; from *L. sungi* by ventral coloration, male body size and iris coloration; from *L. tuberosus* by ventral coloration, presence of black supratympanic line and skin texture; from *L. ventripunctatus* by ventral coloration and iris coloration; and from *L. zhangyangpingi* by ventral coloration, male body size and iris coloration. See Table 8 for details.

From members of the *L. applebyi* group, *L. tadungensis* **sp. nov**. differs from all species by at least one morphological character (all following morphometric differences refer to males only). The new species differs from *L. applebyi* by having a significantly greater body size (Wilcoxon post-hoc Z=3.6, p=0.001), greater relative diameter of the eye (Wilcoxon post-hoc Z=2.5, p=0.013), and greater relative pectoral gland size (Wilcoxon post-hoc Z=2.9, p=0.004). *L. tadungensis* **sp. nov**. differs from *L. bidoupensis* by having a significantly smaller relative head width (Wilcoxon post-hoc Z=-2.1, p=0.032), smaller relative distance between eye and tympanum (Wilcoxon post-hoc Z=-2.1, p=0.032), and gold iris (versus reddish upper and silver below in *L. bidoupensis*). *L. tadungensis* **sp. nov**. differs from *L. melicus* by having a significantly larger body size (Wilcoxon post-hoc Z=3.5, p=0.001), and smaller relative tibia length (Wilcoxon post-hoc Z= -2.3, p=0.019). *L. tadungensis* **sp. nov**. differs from *L. pyrrhops* by having a significantly smaller body size (Wilcoxon post-hoc Z= -3.4, p=0.001), smaller relative tibia length (Wilcoxon post-hoc Z= -3.2, p=0.002), smaller relative distance between eye and tympanum (Wilcoxon post-hoc Z=-3.1, p=0.002) and smaller relative diameter of the eye (Wilcoxon post-hoc Z= -3.3, p=0.001). *L. tadungensis* **sp. nov**. differs from *L. ardens* **sp. nov.** by having a significantly larger body size (Wilcoxon post-hoc Z= 3.4, p=0.001) and smaller relative tibia length (Wilcoxon post-hoc Z= -3.0, p=0.003). *L. tadungensis* **sp. nov**. differs from *L. pallidus* **sp. nov.** by having smaller relative tibia length (Wilcoxon post-hoc Z= -3.1, p=0.002), smaller relative distance between eye and tympanum (Wilcoxon post-hoc Z= -2.4, p=0.019), a black supratympanic line (versus no black supratypmanic line in *L. pallidus* **sp. nov**) and mostly smooth skin texture (versus tuberculate in *L. pallidus* **sp. nov**). *L. tadungensis* **sp. nov**. differs from *L. kalonensis* **sp. nov.** by having a significantly smaller body size (Wilcoxon post-hoc Z= -3.3, p=0.001) and smaller relative tibia length (Wilcoxon post-hoc Z= -3.4, p=0.001). *L. tadungensis* **sp. nov**. differs from *L. maculosus* **sp. nov.** by having a significantly smaller relative tibia length (Wilcoxon post-hoc Z= -2.5, p=0.013). See Table 4 and Fig. 4.

The male advertisement call of *L. tadungensis* **sp. nov.** differs from all species in the *L. applebyi* group. The call of the new species differs from *L. applebyi* in dominant frequency; from *L. bidoupensis* in having an introductory note present and in dominant frequency; from *L. melicus* in relative length of introductory note and dominant frequency; from *L. pyrrhops* by dominant frequency; from *L. ardens* **sp. nov.** by relative length of introductory note; from from *L. pallidus* **sp. nov.** by call duration and relative length of introductory note; from *L. kalonensis* **sp. nov.** by relative length of introductory note; from *L. maculosus* **sp. nov.** by call duration, number of

notes per call, distinctness of introductory note and different relative duration of introductory note. See Table 7 and Fig. 5–6.

Leptolalax tadungensis **sp. nov.** differs from all species within the *L. applebyi* group by >6.3% divergence at the 16S gene fragment examined. Interspecific variation in four *L. tadungensis* **sp. nov.** collected from up to ~15 km apart was 0.0–0.2%.

Discussion

Species in the *L. applebyi* group are likely to have historically occurred over a large area of hilly northeastern Cambodia, central and southern Vietnam (~30,000 km^2; Rowley *et al*. 2015). However, each species appears to occur over a relatively small area, with mountain ridges and valleys appearing to present barriers to dispersal (Rowley *et al*. 2015). This microendemism is perhaps not surprising given their small body size, specific habitat preferences and thus low dispersal ability. Frogs in the group breed in (and perhaps are more broadly restricted to) small seeps and rivulets, often at or near stream headwaters. This is in contrast to other, generally larger, species of *Leptolalax* most of which breed in larger streams. The specific habitat preferences of the group are likely to further restrict adults to particular drainage basins (as suitable breeding habitat is not present on mountain ridges or valleys), and may limit the probability of larval dispersal along streams (except perhaps in high rainfall events).

Habitat loss is the greatest threat to amphibians in Southeast Asia, and the amphibians of the region appear to be particularly vulnerable to habitat alterations (Rowley *et al*. 2010d). Range-restricted species such as species in the *L. applebyi* group are likely to be most at risk (Rowley *et al.* 2010d), and frogs of the *L. applebyi* group appear to be restricted to relatively undisturbed broadleaf evergreen forest. A considerable portion of their historical range is likely to have already been lost due to deforestation (Rowley *et al*. 2005) and habitat loss and modification is a continued threat in the region (Meyfroidt & Lambin, 2008).

This study confirms significant species richness underestimation in the *Leptolalax applebyi* species group. The five additional species named herein almost triple the known species diversity in a group of frogs first identified in only 2009 (Rowley & Cao 2009). Further diversity in this group is likely to be revealed with additional surveys, particularly in drainage basins adjacent to known species. In particular, 'Lineage 7' of the *L. applebyi* group (Rowley *et al*. 2015) is likely to be a new species, and additional material and/or call recordings are needed to confirm this. Due to rapid and ongoing deforestation, species in this group are at great risk of disappearing before they are even discovered (Rowley *et al*. 2015). Further survey work and additional systematic work to understand the true diversity of amphibians in the region is urgently required for effective conservation management.

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Development issued permission to collect (Permit number 3023/GT-BNN-KL & 1430/GT-BNN-KL) for Lam Dong Province, Vietnam. The Vietnamese Ministry of Agriculture and Rural Development (Permit number 779/TCLN-BTTN and Export Permit No. 11VN0003N/KL-NC) for work in Binh Thuan Province. The Directorate of Forest Protection Department and Department of Agriculture and Rural Development of Binh Thuan and Dak Nong provinces supported our fieldwork. Mr Nguyen Cong Van, Director of Phuoc Binh National Park permitted us to work in Ninh Thuan Province, Vietnam (University of Science document 425/KHTN-KH and 494/KHTN-KH). Field work was facilitated by Conservation International, The Institute of Ecology and Biological Resources, the Australian Museum, World Wildlife Fund Greater Mekong, and managers and staff at protected areas surveyed. David Kizirian from the American Museum of Natural History and students from the Faculty of Biology-Biotechnology, University of Science, Ho Chi Minh City were invaluable in the field. Jimmy A. McGuire, Bryan L. Stuart, Carol Spencer, Cuong The Pham, Prof. Dr. Wolfgang Böhme and David Kizirian, loaned specimens and/or tissues in their care. Ross Sadlier and Cecilie Beatson provided support to JR.

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APPENDIX I. Comparative material examined.

***Leptolalax aereus**:* Laos, Savannakhet Province, Vilabouli District (NCSM 76038–76057, 76061–76071; SAMA R64234–64242; type specimens).

***Leptolalax applebyi**:* Vietnam, Quang Nam Province, Song Thanh Nature Reserve (AMS R 171703–171707; type specimens). Vietnam, Kon Tum Province, Ngoc Linh Nature Reserve (AMS R 173635, 177637, UNS 00462/AMS R 173776, AMS R 173777, AMS R 173778, UNS 00465/AMS R 173780, AMS R 176528, UNS 00464/AMS R 176529, UNS 00465/AMS R 176530, AMS R 176531–176533).

Leptolalax bidoupensis: Vietnam, Lam Dong Province, Bidoup–Nui Ba National Park (AMS R 173133, UNS 00101/AMS R 173135, UNS 00102/AMS R 173137, AMS R 173134, AMS R 173136, NCSM 77320, NCSM 77321, NCSM 77322; type specimens).

***Leptolalax botsfordi**:* Vietnam, Lao Cai Province, Hoang Lien National Park (VNMN 03682, AMS R 176534–176541; type specimens).

Leptolalax croceus: Vietnam, Kon Tum Province, Ngoc Linh Nature Reserve (AMS R 173738–173748, UNS 00108/ AMS R 173750, AMS R 173751, UNS 00109/AMS R 173752, UNS 00110/AMS R 173775, UNS 00111/AMS R 173779; type specimens).

Leptolalax eos: Laos, Phongsaly Province (FMNH 258052–258064, 258066). Laos, Luang Namtha Province (FMNH 271281–271285).

Leptolalax firthi: Vietnam, Kon Tum Province, Ngoc Linh Nature Reserve (AMS R 176524, AMS R 176525, UNS 00460/ AMS R 176526, UNS 00461/AMS R 176527, AMS R 176513, UNS 00456/AMS R 176514, AMS R 176515, NCSM 78995, AMS R 176503–176507, UNS 00453/AMS R 176509, UNS 00454/AMS R 176510, UNS 00455/AMS R 176511, AMS R 176500, UNS 00452/AMS R 176501, AMS R 176502, AMS R 176508, AMS R 1765012, AMS R 176517, NCSM 78996–78997, AMS R 176518, UNS 00457/AMS R 176516, AMS R 176520, AMS R 176522, UNS 00458/AMS R 176519, AMS R 176521, UNS 00459/AMS R 176523, AMS R 173736, AMS R 173774). Vietnam, Quang Nam Province, Song Thanh Proposed Nature Reserve (AMS R 171714, AMS R 171722)

***Leptolalax liui**:* China, Fukien (Fujian) Province, Ch'ungsan, Hsein (AMNH A30127, 30129, 30130, 30135; FMNH 22415–22418; topotypes). China, Fujian Province, Yenping (AMNH A28417).

Leptolalax melicus: Cambodia, Ratanakiri Province, Virachey National Park (MVZ 258074–258077, MVZ 258197– 258199; type specimens).

Leptolalax nyx: Vietnam, Ha Giang Province (AMNH A163798, 163799, 163802–163804, 163811–163813, 163817–163819, 163822–163824, 163828–163830; topotypes).

Leptolalax oshanensis: China, Sichuan Province, Hongya Xian (FMNH 232907–232921; ~50 km from type locality).

***Leptolalax sungi**:* Vietnam, Lao Cai Province (AMNH 168676).

Leptolalax tuberosus: Vietnam, Quang Nam Province, Song Thanh Nature Reserve (AMS R 171715–171721). Vietnam, Quang Nam Province (AMNH A163665).

***Leptolalax ventripunctatus**:* Laos, Phongsaly Province (FMNH 258077). Laos, Luang Namtha Province (FMNH 271317–21, 271329, 271331).