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## A new species of *Leptolalax* (Anura: Megophryidae) from Laos

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### Abstract

We describe a new species of megophryid frog in the genus *Leptolalax* from southern Laos. *Leptolalax aereus* **sp. nov.** is distinguished from its congeners by a combination of size (25.1–28.9 mm in 28 adult males, 27.1–38.6 mm in 12 adult females), absence of distinct black or dark brown dorsolateral markings on head, near immaculate white chest and belly, head length greater than head width, no webbing or lateral fringing on fingers, rudimentary webbing between toes I–IV and no webbing between toes IV–V, toes with weak lateral fringing, and a call consisting of an average of 3–4 notes containing 1–2 pulses, and with a dominant frequency of 6187.5–7875 Hz. The new species is associated with rocky streams in semi-evergreen and evergreen forest between 284–511 m elevation.

**Key words:** Acoustics, Anura, *Leptolalax aereus* **sp. nov.**, Laos, Southeast Asia, Indochina

### Introduction

The genus *Leptolalax* (Dubois 1983) is a group of relatively small, cryptic frogs associated with rocky streams in hilly evergreen forests (Frost 2010; Rowley *et al.* 2010a; Rowley *et al.* 2010b). Distributed throughout Southeast Asia, southern China and northeastern India, the genus *Leptolalax* currently includes 28 species (Frost 2010; Rowley *et al.* 2010a; Rowley *et al.* 2010b). Additional regional field surveys and the incorporation of acoustic and molecular data to more rigorously assess the delineation of species boundaries has resulted in more than an eight-fold increase in the number of known *Leptolalax* species since the genus was described by Dubois (1983) (Frost 2010; Rowley *et al.* 2010a; Rowley *et al.* 2010b).

Ten species of *Leptolalax* have been reported to occur in Indochina; *L. applebyi*, *L. bourreti*, *L. croceus*, *L. melicus*, *L. nahangensis*, *L. oshanensis*, *L. pelodytoides*, *L. pluvialis*, *L. sungi* and *L. tuberosus* (Frost 2010; Rowley *et al.* 2010a; Rowley *et al.* 2010b). To date, only two species of *Leptolalax*, *L. bourreti* and *L. oshanensis*, have been reported from Laos (Stuart 2005; Frost 2010). Here we describe a new species of *Leptolalax* collected during recent herpetological surveys in southern Laos.

### Material and methods

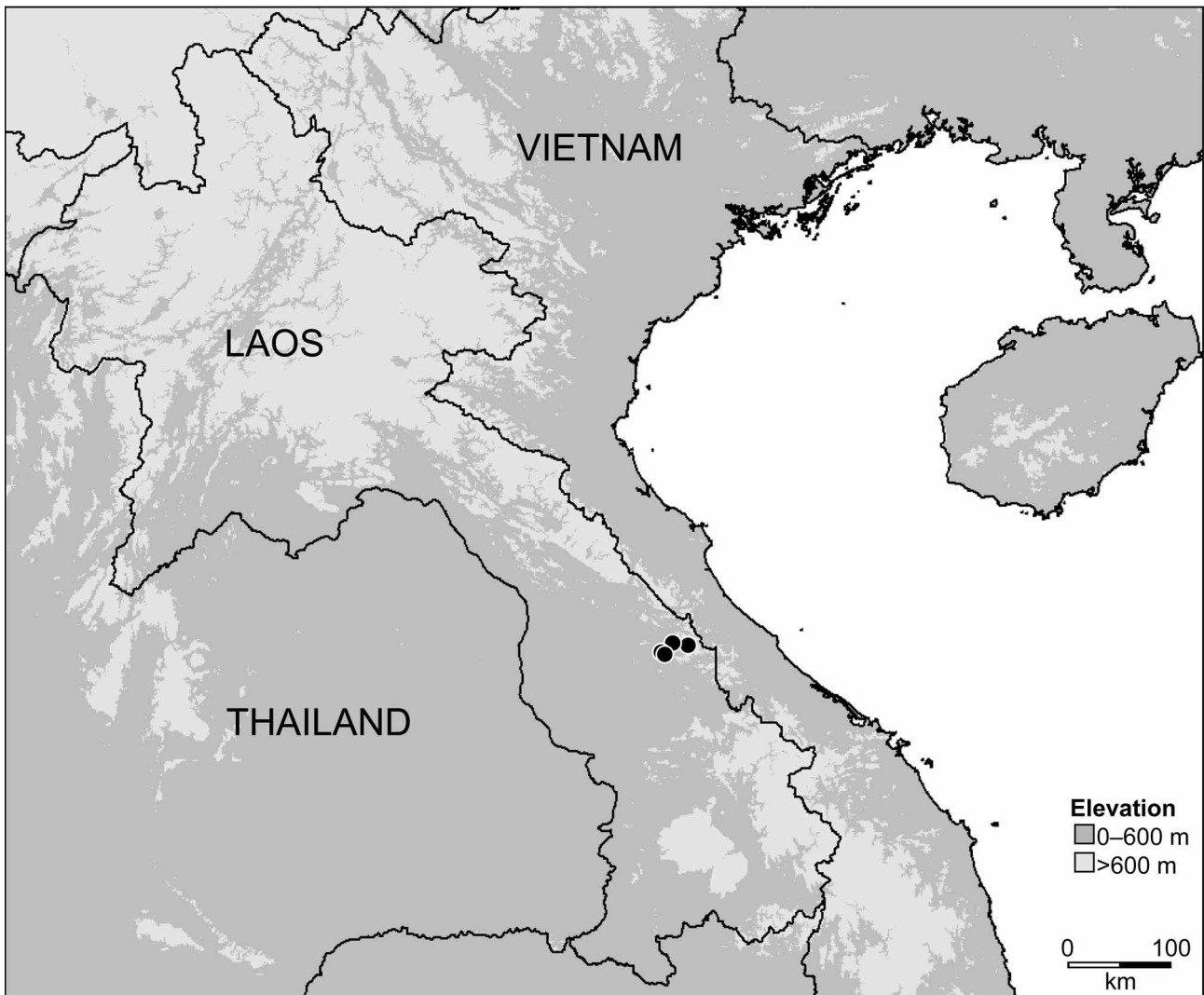
We recorded morphological data from specimens fixed in 10% formalin and then stored in 70% ethanol. Specimens were deposited at the North Carolina Museum of Natural Sciences (NCSM) and the South Australian Museum (SAMA). Morphometric data were taken (to the nearest 0.1 mm) with digital calipers. Measurements include snout-vent length (SVL); head length from tip of snout to rear of jaws (HDL); head

width at the 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), length of adpressed first finger from tip to distal edge of the inner palmar tubercle (FIL), length of adpressed second finger from tip to distal edge of inner palmar tubercle (F2L), and length of adpressed third finger from tip to distal edge of inner palmar tubercle (F3L). We use a traditional formula for finger numbering rather than one based on homology (eg. Alberch & Gale 1985). Sex was determined by direct observation of calling in life and the presence of internal vocal sac openings. We obtained comparative morphological data from museum specimens (Appendix 1) and from the literature: *L. alpinis* (Fei *et al.* 1991; Fei *et al.* 2009), *L. applebyi* (Rowley & Cao 2009), *L. arayai* (Matsui 1997), *L. bourreti* (Dubois 1983), *L. croceus* (Rowley *et al.* 2010a), *L. dringi* (Dubois 1986, Inger & Stuebing 2005), *L. fuliginosus* (Matsui 2006), *L. gracilis* (Günther 1872; Malkmus *et al.* 2002; Inger & Stuebing 2005), *L. hamidi* (Matsui 1997), *L. heteropus* (Boulenger 1900), *L. kecil* (Matsui *et al.* 2009), *L. khasiorum* (Das *et al.* 2010), *L. kajangensis* (Grismer *et al.* 2004), *L. lateralis* (Anderson 1871; Humtsoe *et al.* 2008), *L. liui* (Fei *et al.* 1991; Fei *et al.* 2009), *L. maurus* (Inger *et al.* 1997), *L. melanoleucus* (Matsui 2006), *L. melicus* (Rowley *et al.* 2010b), *L. nahangensis* (Lathrop *et al.* 1998), *L. oshanensis* (Lui 1950; Fei *et al.* 2009), *L. pelodytoides* (Boulenger 1893), *L. pictus* (Malkmus 1992; Malkmus *et al.* 2002), *L. pluvialis* (Ohler *et al.* 2000), *L. solus* (Matsui 2006), *L. sungi* (Lathrop *et al.* 1998), *L. tamdil* (Sengupta *et al.* 2010), *L. tuberosus* (Inger *et al.* 1999; Rowley *et al.* 2010a), *L. ventripunctatus* (Fei *et al.* 1991; Fei *et al.* 2009). We also examined colour photographs of the holotype of *L. pluvialis* (MNHN 199.5675) in preservative.

Advertisement calls were recorded with an Edirol R-09 WAVE/MP3 Recorder with a Røde NTG-2 condenser shotgun microphone (96 kHz sampling rate and 24-bit encoding) or a TCM-5000 Tape Recorder with a Sennheiser ME66 microphone (48 kHz sampling rate and 16-bit encoding). Calls were recorded at a distance of approximately 0.2–0.5 m and ambient temperatures were taken immediately after recordings using a Kestrel 3500 hand-held weather meter or a HLP Digital Pocket Thermometer. Calls were analysed with Raven Pro 1.3<sup>®</sup> software (<http://www.birds.cornell.edu/raven>). Audiospectrograms in figures were calculated with fast-Fourier transform (FFT) of 256 points, 50% overlap and 172 Hz grid-spacing, using Hanning windows. Comparisons of advertisement calls among species within the genus *Leptolalax* are complicated by inconsistent use of terms and a lack of clear definitions in terminology, particularly with respect to the units of a call, a note or a pulse. Here we use the definitions of Duellman (1970), except that we define a single call as vocalisations produced during a single expiration (Brown & Richards 2008), and use the term ‘call group’ to refer to temporal groups of calls, separated by intervals of silence distinctly greater than those between calls. 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 20 calls per individual we measured the call duration (ms), intercall interval (ms), number of notes per call, note duration (ms), internote interval (ms), number of pulses per note, note repetition rate (notes/s) and dominant frequency (Hz). Comparative advertisement call characters for *Leptolalax* species were taken from references (Jiang *et al.* 2002; Malkmus *et al.* 2002; Matsui 1997, 2006; Matsui *et al.* 2009; Xu *et al.* 2005; Rowley & Cao 2009; Rowley *et al.* 2010a; Rowley *et al.* 2010b). To maintain consistency, we have used the terminology defined above to compare calls, regardless of terms used in these references.

### ***Leptolalax aereus* sp. nov.**

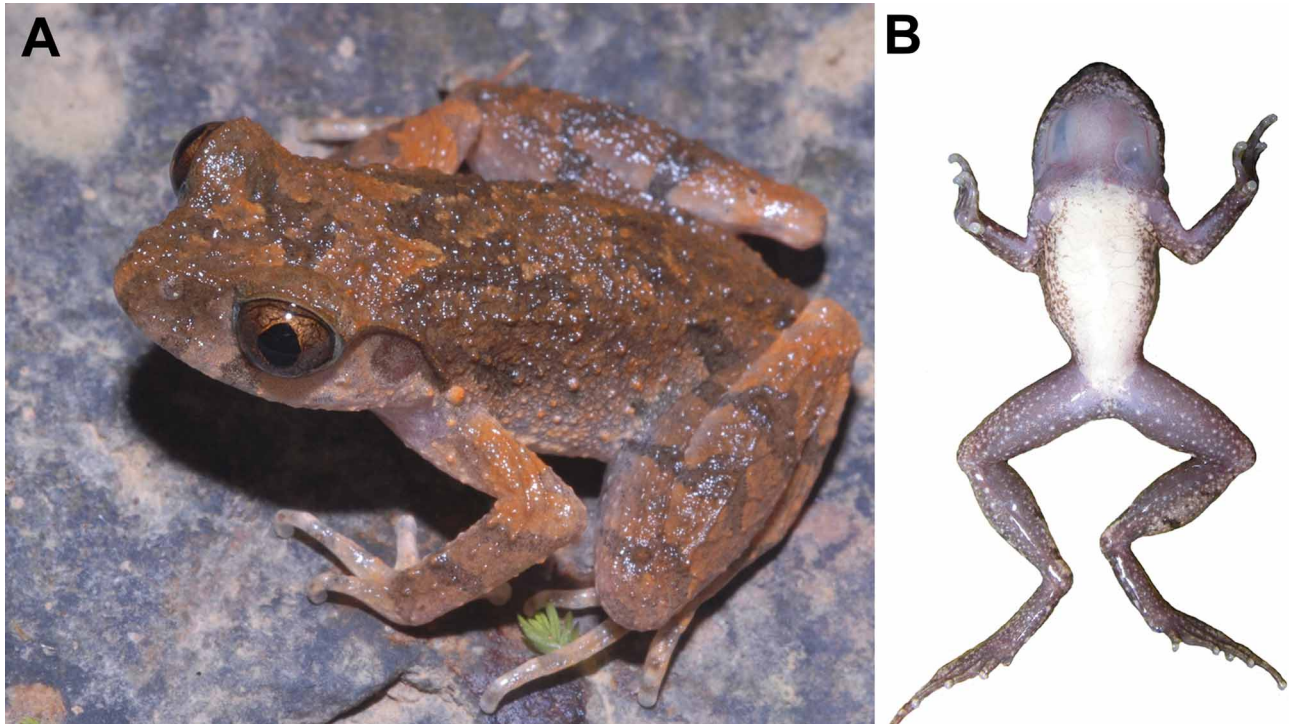
**Holotype:** SAMA R64236, adult male, calling on mid-stream rock pile in 6 m wide, swift rocky stream in semi-evergreen forest in the Sepon Mining Tenement, Vilabouli District, Savannakhet Province, Laos (16.96317° N, 106.0466° E, 326 m), collected at 21:36 h on 23 November 2008 by B. L. Stuart, S. J. Richards, S. Phimmachak and N. Sivongxay.



**FIGURE 1.** Collection sites of *Leptolalax aereus* sp. nov.

**Paratypes:** NCSM 76038, SAMA R64234–64235 (three males), same data as holotype but collected near a swift, rocky stream. SAMA R64237 (one male), same locality data as holotype but collected on 25 November 2008. NCSM 76041–76044 (four males) and NCSM 76039–76040, SAMA R64238–63240 (five females), from the Sepon Mining Tenement, Vilabouli District, Savannakhet Province, Laos (16.95653° N, 106.0677° E, 303 m), collected on 26 November 2008; NCSM 76045 (female), and SAMA R64241 (male), collected at same site on 28 November 2008; NCSM 76046 (female) collected at same site on 30 November 2008. NCSM 76047 (male) from the Sepon Mining Tenement, Vilabouli District, Savannakhet Province, Laos (16.03939° N, 106.1567° E, 284 m), collected on 7 December 2008. SAMA R64242 (male) from the Sepon Mining Tenement, Province, Laos (17.011806° N, 106.220139° E, 353 m), collected on 6 December 2008. NCSM 76049–76051 (three males) and NCSM 76048 (female) from the Sangi River drainage basin, Vilabouli District, Savannakhet Province, Laos (17.02141° N, 106.2904° E, 474 m), collected on 22 June 2009; NCSM 76053 (male) collected at same site on 23 June 3009; NCSM 76054–76056 (three males) and NCSM 76061 (female) collected at same site on 24 June 2009. NCSM 76052 (male) from the Sangi River drainage basin, Vilabouli District, Savannakhet Province, Laos (17.02161° N, 106.2890° E, 450 m), collected on 23 June 2009; NCSM 76065 (male) and NCSM 76066 (female) collected from same site on 29 June, 2009. NCSM 76057 (female) from the Sangi River drainage basin, Vilabouli District, Savannakhet Province, Laos (17.0257° N, 106.2944° E, 511 m), collected on 24 June 2009. NCSM 76062 (male) from the Sangi River drainage basin, Vilabouli District, Savannakhet Province, Laos (17.01874° N, 106.2973° E, 465 m), collected

on 25 June, 2009. NCSM 76063 (female) and NCSM 76064 (male) from the Sangi River drainage basin, Vilabouli District, Savannakhet Province, Laos (17.02345° N, 106.2894° E, 438 m), collected on 26 June 2009. NCSM 76067–76069 (three males) from the Sangi River drainage basin, Vilabouli District, Savannakhet Province, Laos (16.01816° N, 106.2973° E, 470 m), collected on 30 June 2009. NCSM 76070–76071 (two males) from the Sangi River drainage basin, Vilabouli District, Savannakhet Province, Laos (17.02073° N, 106.2862° E, 454 m), collected on 1 July 2009. Specimens from 2008 were collected by B. L. Stuart, S. J. Richards, S. Phimmachak and N. Sivongxay. Specimens from 2009 were collected by B. L. Stuart, S. Phimmachak and N. Sivongxay.



**FIGURE 2.** *Leptotalax aereus* sp. nov. in life. (A) Dorsolateral view in the field of male holotype SAMA R64236, (B) ventral view of male paratype NCSM 76064.

**Etymology.** Specific epithet from *aereus* L., meaning made of copper or bronze; in reference to copper hue evident in life on the dorsal surface of most specimens.

**Diagnosis.** Assigned to the genus *Leptotalax* on the basis of the following: 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, ventrolateral and femoral glands), vomerine teeth absent, tubercles on eyelids, anterior tip of snout with pale, vertical bar (Dubois 1980; Lathrop *et al.* 1998; Delorme *et al.* 2006). *Leptotalax aereus* sp. nov. is distinguished from its congeners by a combination of (1) size (25.1–28.9 mm in 28 adult males, 27.1–38.6 mm in 12 adult females), (2) absence of distinct black or dark brown dorsolateral markings on head, (3) near immaculate white chest and belly, (4) head length greater than head width, (5) no webbing or lateral fringing on fingers, (6) rudimentary webbing between toes I–IV, no webbing between toes IV–V; toes with very weak lateral fringing, (7) a call consisting of an average of 3–4 notes containing 1–2 pulses, and with a dominant frequency of 6187.5–7875 Hz.

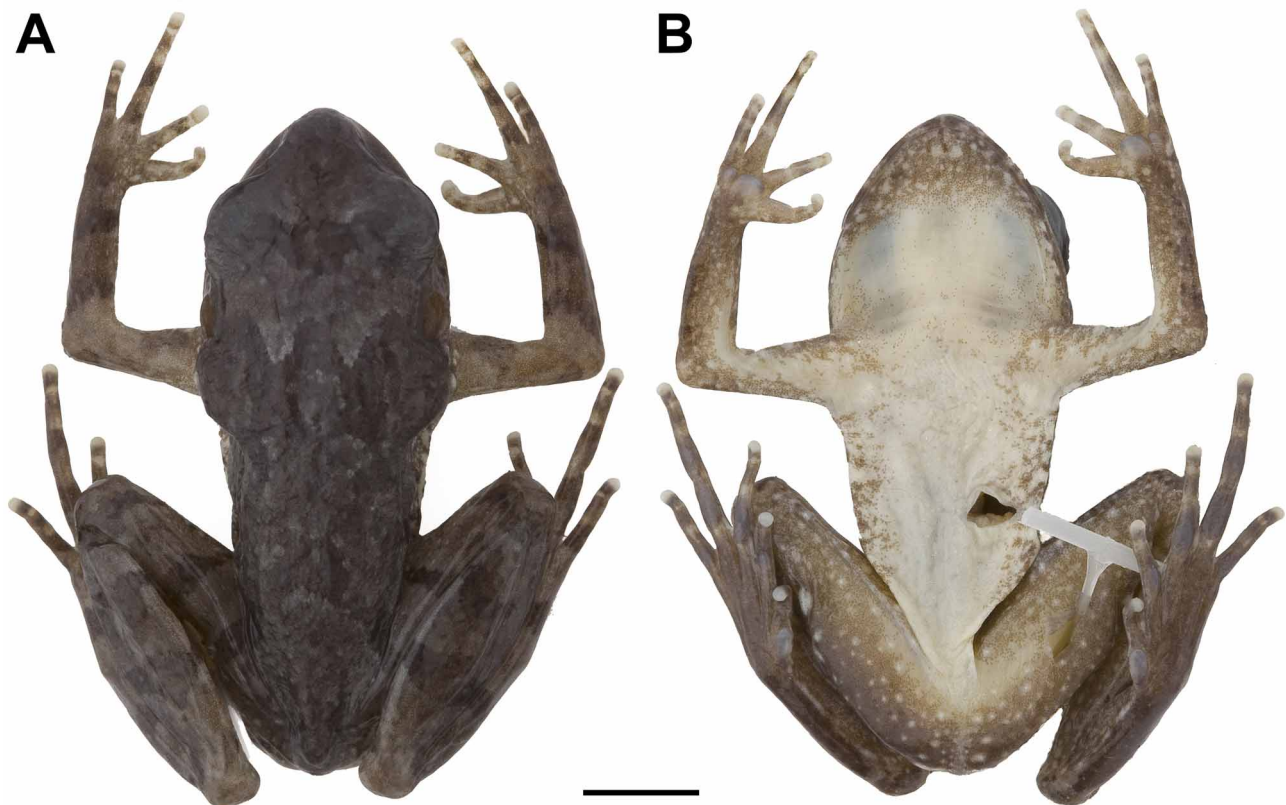
**Description of holotype.** Head longer than wide; snout rounded in profile, projecting slightly over lower jaw; nostril closer to tip of snout than eye; canthus rostralis rounded; lores sloping; vertical pupil; eye diameter approximately equal to snout length; tympanum distinct, round, diameter 56% that of the eye, tympanic annulus not elevated relative to skin of temporal region; vomerine teeth absent; pineal ocellus absent; vocal sac openings large, oval, located laterally on floor of mouth; paired internal subgular vocal sac; tongue large, broad, with small notch at narrowed, posterior tip; distinct, raised supratympanic ridge running from eye towards axillary gland. Tips of fingers rounded, not broader than phalanges; finger I almost as long



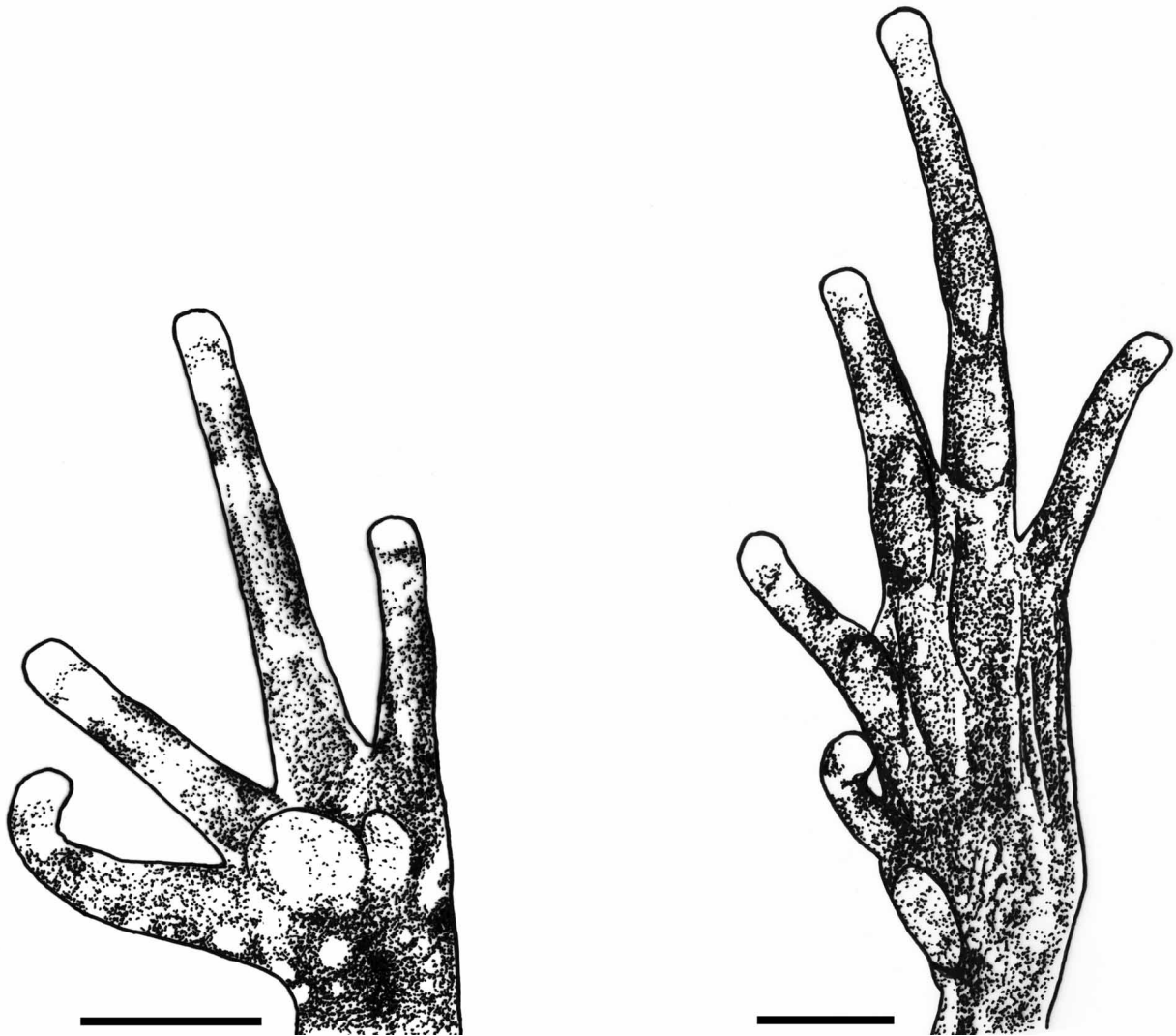
as finger II, relative finger lengths  $I < II = IV < III$ ; nuptial pads absent; subarticular tubercles absent; a large, laterally compressed inner palmar tubercle distinctly separated from smaller, laterally compressed outer palmar tubercle; no finger webbing or lateral fringes. Tips of toes like fingers; relative toe length  $I < II < V < III < IV$ ; subarticular tubercles absent, replaced by dermal ridges, distinct on second, third, fourth and fifth toes; small, oval inner metatarsal tubercle pronounced, outer metatarsal tubercle absent; webbing rudimentary between toes I–IV, absent between toes IV–V; toes with very weak lateral fringing. Tibia approximately half that of snout-vent length; tibiotarsal articulation reaches to tip of snout. Skin on entire dorsum with low, round or laterally compressed tubercles, more frequent and larger on posteriodorsal and dorsolateral surfaces, forming faint ridges on dorsal surface of thighs and upper arms; ventral skin smooth; pectoral gland laterally compressed, 1.0 mm diameter; femoral gland oval, 0.9 mm diameter, on posteroventral surface of thigh, closer to knee than to vent; supra-axillary gland raised, 0.8 mm diameter; many small glands around cloacal opening. Ventrolateral glands present, dorsolaterally compressed, forming an incomplete line.

**Colour of holotype in life.** Dorsum brown with copper/orange wash, axilla to elbows and heel orange. Dorsal surface of head pale copper. Darker greyish-brown interorbital bar, W-shaped marking between axillae, inverted V-shaped marking between sacrum, darkening towards inguinal region; pale greyish-brown bars on background of pale orange on upper lip; loreal and tympanic region with no distinct dark brown or black markings; diffuse, transverse greyish-brown bars on dorsal surface of limbs; ventral surface of elbow and upper arm without dark bars; fingers and toes with faint transverse barring. Small greyish-brown flecks along flanks. Ventral surface of chest and belly opaque white; throat transparent pale pink; outer edges of chin, and thighs, arms and all of tibiotarsus brownish grey with small whitish spots. Supra-axillary gland orange; femoral, pectoral and dorsolateral glands white. Iris bronze with minute, black reticulations.

**Colour of holotype in preservative.** Dorsal surface brown; ventral surface, including throat, white. Ventrolateral margins of chest and belly and margins of throat with brown speckling. Ventral surfaces of thighs and arms cream to pale brown with white speckling. Dark greyish brown and white flecks on flanks. White macroglands and pectoral glands have become indistinct in preservative.



**FIGURE 3.** (A) Dorsal and (B) ventral view of preserved holotype (SAMA R64236) of *Leptolalax aereus* sp. nov. Scale bar = 5 mm.



**FIGURE 4.** Ventral surfaces of left hand and left foot of preserved holotype of *Leptolalax aereus* sp. nov. (SAMA R64236). Scale bars = 2 mm.

**Measurements.** Holotype: SVL 28.7, HDL 11.0, HDW 10.2, SNT 4.2, EYE 3.6, IOD 3.2, TMP 2.0, TEY 1.0, TIB 14.6, ML 7.5, PL 14.1, F1L 3.1, F2L 3.5, F3L 5.9.

**Variation.** Colour of paratypes varied slightly in life. NCSM 76065 and SAMA R64242 had more extensive dusting or spotting on throat and lateral margins of belly than holotype. Colour of NCSM 76054 appears aberrant among the type series, exhibiting large black patches on ventral surfaces of legs, chest and throat. Some individuals have slightly more extensive webbing (NCSM 76039, NCSM 76043, NCSM 76045, NCSM 76064, SAMA R64239, SAMA R64242) or lateral fringing (NCSM 64242) on feet. Ventrolateral glandular lines vary in degree of completeness and distinctiveness, and are indistinct in SAMA R64242, NCSM 76048, NCSM 76046, NCSM 76049, NCSM 76057, NCSM 76062, and NCSM 76065. Glands around cloacal opening vary in size and number. Skin less tuberculate in preservative than in life. In preservative dorsal skin texture varies from finely tuberculate (NCSM 76040, NCSM 76044–76045, NCSM 76048, NCSM 76066, NCSM 76068, SAMA R64239) to almost smooth (NCSM 76038, NCSM 76041–76043, NCSM 76047, NCSM 76049–76050, NCSM 76052, NCSM 76054, NCSM 76056–76057, NCSM 76061–76063, NCSM 76069–76071, SAMA R64234–64238, 64240–64242). Females are significantly larger than males (Mann-Whitney *U*-test,  $Z = -4.460$ ,  $p < 0.001$ ;  $N = 40$ ), and in life, have opaque whitish throats, compared to transparent pale pink throats of males. Measurements of the type series are shown in Table 1.

**TABLE 1.** Measurements (mm) of adult *Leptolalax aereus* sp. nov. Abbreviations defined in text.

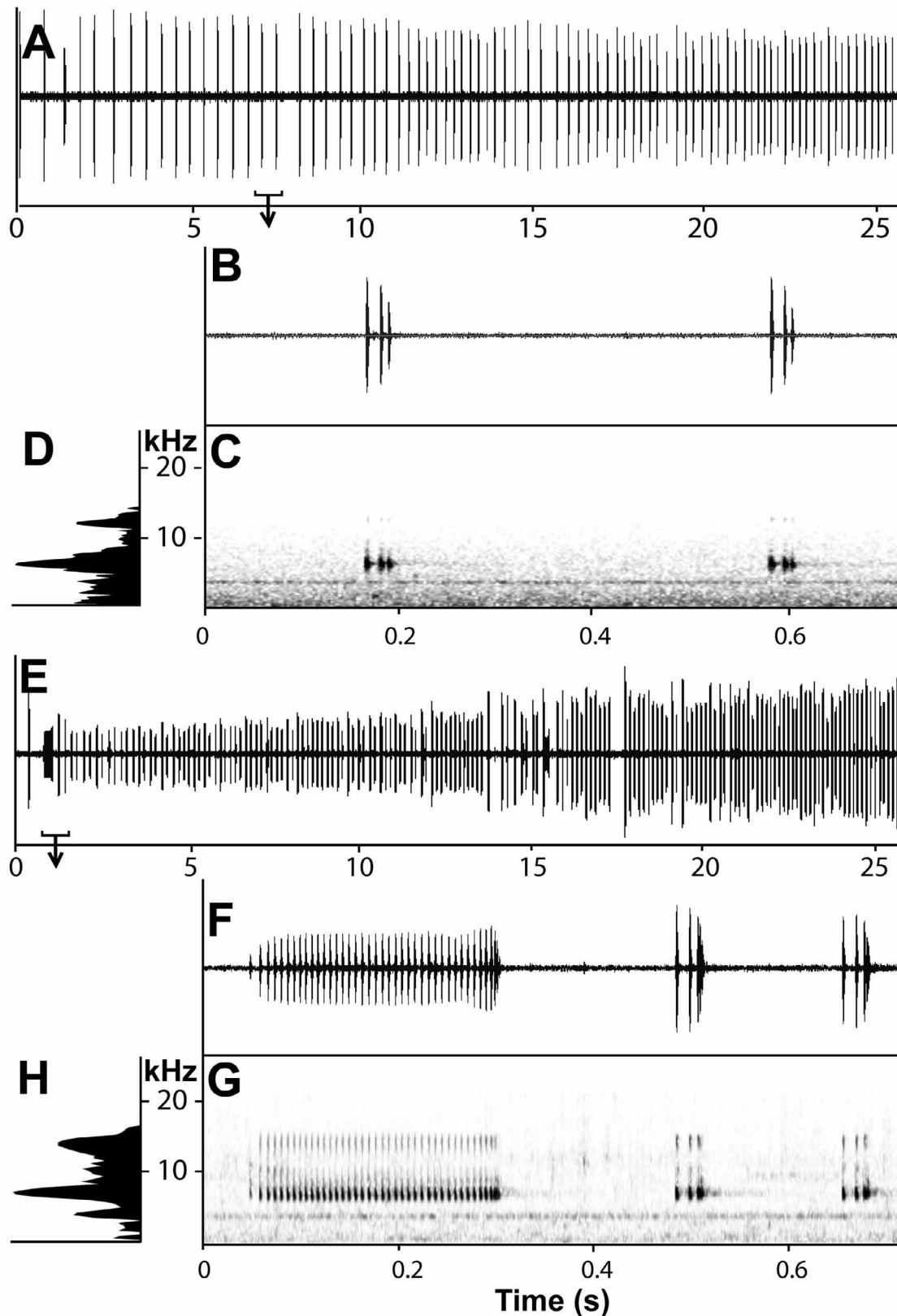
Measurements	Males	Females
	Range; Mean $\pm$ S. D. (N=26)	Range; Mean $\pm$ S. D. (N=12)
SVL	25.1–28.9; 27.3 $\pm$ 0.9	27.1–38.6; 34.7 $\pm$ 2.9
HDL	9.6–11.0; 10.2 $\pm$ 0.3	10.2–13.7; 12.8 $\pm$ 0.9
HDW	8.8–10.2; 9.5 $\pm$ 0.3	9.6–13.1; 12.1 $\pm$ 0.9
SNT	3.3–4.2; 3.8 $\pm$ 0.2	3.7–5.3; 4.5 $\pm$ 0.4
EYE	3.0–3.9; 3.4 $\pm$ 0.2	3.1–5.1; 4.1 $\pm$ 0.5
IOD	2.2–3.5; 2.8 $\pm$ 0.3	2.9–3.6; 3.2 $\pm$ 0.2
TMP	1.6–2.0; 1.8 $\pm$ 0.1	1.9–2.4; 2.2 $\pm$ 0.1
TEY	0.6–1.2; 0.9 $\pm$ 0.1	0.9–1.6; 1.3 $\pm$ 0.2
TIB	12.8–14.7; 13.8 $\pm$ 0.5	13.1–18.6; 16.9 $\pm$ 1.3
ML	6.3–7.5; 7.0 $\pm$ 0.3	6.6–9.2; 8.3 $\pm$ 0.7
PL	12.1–14.1; 13.0 $\pm$ 0.6	12.8–17.7; 15.8 $\pm$ 1.3
F1L	2.3–3.1; 2.7 $\pm$ 0.2	2.5–3.9; 3.4 $\pm$ 0.4
F2L	2.6–3.5; 3.0 $\pm$ 0.2	2.9–4.3; 3.7 $\pm$ 0.3
F3L	4.6–6.8; 5.7 $\pm$ 0.4	5.3–7.5; 6.9 $\pm$ 0.6
	Range; Median (N=26)	Range; Median (N=12)
TIB:SVL	0.48–0.53; 0.50	0.46–0.53; 0.49
HDL:SVL	0.36–0.39; 0.37	0.34–0.38; 0.37
HDL:HDW	1.03–1.14; 1.07	1.05–1.08; 1.06

**Advertisement call.** Call descriptions are based on the calls of the holotype (SAMA R64236), recorded at 22.4°C ambient temperature (Table 2, Figures 5A–D). Calls were approximately 30 ms in duration, and repeated at a variable rate, averaging approximately six calls per second. Each call consisted of three, or occasionally four notes of 6–9 ms duration, and each note contained 1–2 pulses. Within each call, notes were repeated at a rate of approximately 40–45 notes per second. The dominant frequency of the calls was 6187.5–6375 Hz, however energy was spread over a fairly wide band (5500–7000 Hz). Faint harmonics were detected at approximately 12750 Hz, and the fundamental frequency was absent (Figure 5C). Frequency modulation was weak or absent, with successive notes often declining slightly in frequency in the order of 100–200 Hz. Amplitude modulation was present, with calls tending to decline in intensity with successive notes. The advertisement call of paratype NCSM 76068, taken at 25.5°C ambient temperature, had a higher note repetition rate and was more variable than that of SAMA R64236 (Figures 5E–H). Call interval, call rate and the number of notes within each call were highly variable both within and among individuals (N=6, Table 2). Although the intensity and rate of calling increased and decreased during bouts of calling in all recordings, calls did not form distinct call groups (in up to 204 s of calling). The dominant frequency was positively correlated with temperature (Figure 6). To the human ear, the advertisement call of *L. aereus* is a high-pitched, rapid chirping, sounding similar to an orthopteran.

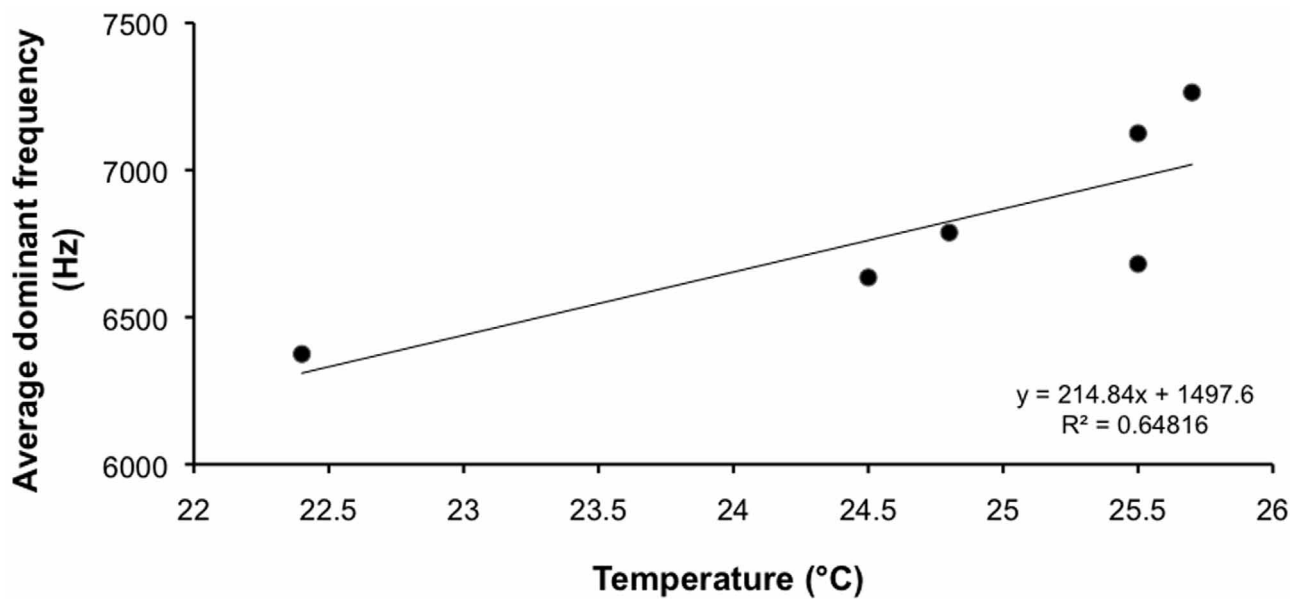
**Ecology.** *Leptolalax aereus* was abundant at rocky streams in closed evergreen or semi-evergreen forest. All known locations are between 284–511 m elevation, and animals were collected at night between 20:25–23:15 h. Males were observed calling from crevices between boulders, on rocks, and on stream banks. Females were found on rocks mid-stream, and up to 1 m from the streams. *Leptolalax aereus* was heard calling in both June and November, suggesting that breeding may occur throughout the year.

**Conservation status.** To date, the new species is only known from Vilabouli District, Savannakhet Province, Laos, but it probably occurs in other suitable habitats in adjoining areas of Laos and Vietnam. Although it appears to require closed evergreen or semi-evergreen forest along the streams where it occurs, several of the streams where we documented this species run through severely degraded habitats, suggesting





**FIGURE 5.** The advertisement call of *Leptolalax aereus* **sp. nov.** holotype SAMA R64236, recorded at ambient air temperature of 22.4°C (A) 25 s waveform of relative amplitude, (B) an expanded 0.7 s waveform, and (C) corresponding 0.7 s spectrogram showing two representative calls, and (D) a power spectrum (relative amplitude vs. frequency). The advertisement call of *Leptolalax aereus* **sp. nov.** paratype NCMS 76068, recorded at 25.5 °C. (E) 25 s waveform of relative amplitude, (F) an expanded 0.7 s waveform, and (G) corresponding 0.7 s spectrogram showing three representative calls, and (H) power spectrum (relative amplitude vs. frequency).



**FIGURE 6.** Temperature-dependence of the average dominant frequency of the advertisement call of *Leptotalax aereus* sp. nov.

**TABLE 2.** Measurements of advertisement call parameters for *Leptotalax aereus* sp. nov. Parameter values are given as means (and ranges).

	SAMA R64236*	NCSM 76054	NCSM 76064	NCSM 76065	NCSM 76067	NCSM 76068
Number of notes measured	59	102	189	62	62	70
Call duration (ms)	26 (16–28)	41.3 (19–100)	77.1 (13–130)	32.7 (29–42)	29.3 (27–37)	33.9 (30–48)
Call repetition rate (calls/s)	3.3	7.4	2.4	6.9	6.4	8
Intercall interval (ms)	273.2 (201–380)	101.4 (78–161)	307 (130–582)	110.3 (92–133)	125.4 (103–154)	85.3 (4–129)
Notes/call	2.95 (2–3)	5.1 (3–13)	9.5 (2–16)	3.1 (3–4)	3.1 (2–4)	3.5 (3–7)
Note duration (ms)	4.0 (3–5)	5.6 (3–19)	3.0 (1–30)	8.3 (4–12)	6.4 (6–9)	4.4 (3–9)
Note repetition rate (notes/s)	75 (63–83)	88 (53–127)	106 (78–129)	64 (59–81)	68 (37–86)	72 (63–133)
Dominant frequency (Hz)	6337.5 (6187.5–6375)	7263.8 (6750–7875)	6787.7 (6575–7500)	6635 (6375–6750)	6681	7125
Temperature (°C)	22.4	25.7	24.8	24.5	25.5	25.5

at least some ability for populations to persist in substantially modified habitats as long as sufficient riparian evergreen forest is retained. Until the distribution and habitat requirements of this species are more adequately documented, we suggest the species should be considered Data Deficient following IUCN's Red List categories (IUCN 2001).

**Comparisons.** *Leptotalax aereus* is a medium-sized species of *Leptotalax* (25.1–28.9 mm in 28 adult males, 27.1–38.6 mm in 12 adult females), and can be distinguished on the basis of size from the smaller *L. applebyi* (males 19.6–20.8 mm, female 21.7 mm), *L. kecil* (males 19.3–20.5 mm, female 25 mm), *L. melicus* (males 19.5–22.7 mm) and *L. pluvialis* (males 21.3–22.3 mm), and the larger *L. bourreti* (male 36.2 mm), *L. gracilis* (males 30–36 mm), *L. kajangensis* (males 34–35 mm), *L. nahangensis* (male 40.8 mm), *L. sungi* (males 48.3–52.7 mm, females 56.7–58.9), and *L. tamdil* (male 32.3 mm, female 31.8 mm).

In lacking distinct dark dorsolateral markings on the head, *L. aereus* can be distinguished from *L. alpinis*, *L. applebyi*, *L. bourreti*, *L. dringi*, *L. fuliginosus*, *L. hamidi*, *L. heteropus*, *L. kajangensis*, *L. khasiorum*, *L. kecil*, *L. melanoleucus*, *L. melicus*, *L. nahangensis*, *L. oshanensis*, *L. pelodytoides*, *L. pictus*, *L. pluvialis*, *L. solus*, *L. sungi* and *L. tamdil*, all of which have dark canthal and/or temporal streaks.

In having an immaculate white chest and belly with only slight darker specking at margins, *L. aereus* can be distinguished from *L. alpinis*, *L. applebyi*, *L. croceus*, *L. dringi*, *L. fuliginosus*, *L. gracilis*, *L. heteropus*, *L. kajangensis*, *L. kecil*, *L. maurus*, *L. melanoleucus*, *L. melicus*, *L. nahangensis*, *L. pluvialis*, *L. solus*, *L. tuberosus* and *L. ventripunctatus*, all of which have dark or otherwise maculate chests and/or bellies.

*Leptotalax aereus*, with a head longer than wide, can be further distinguished from *L. bourreti*, *L. croceus*, *L. khasiorum*, *L. lateralis*, *L. tamdil* and *L. tuberosus*, all of which have heads wider than long. In having rudimentary webbing between toes I–IV, no webbing between toes IV–V; and toes with weak lateral fringing, *L. aereus* can be differentiated from *L. alpinis* and *L. liui*, which have wide lateral fringing on toes, and from *L. pelodytoides*, which has more extensive webbing and wide lateral fringes between toes. The advertisement call of *L. aereus* appears structurally unique among *Leptotalax* in terms of the degree of variability in call interval, call rate and number of notes per call within and among recorded calls. In lacking strong frequency modulation, the call of *L. aereus* differs from *L. dringi* and *L. hamidi*. In having an extremely high frequency (6000–7000 Hz) the call of *L. aereus* can be distinguished from that of *L. applebyi* (3962–4306.6 Hz, 21.5°C), *L. croceus* (2625–3000 Hz, 21.6–25.1°C), *L. fuliginosus* (2250–2430 Hz, 19.3–19.6 °C), *L. gracilis* (2540–2650 Hz, 20°C), *L. heteropus* (2833 Hz, 21°C), *L. kecil* (3200 Hz, 21.4°C), *L. melanoleucus* (3050–3200 Hz, 23.9°C), *L. melicus* (3560–3610 Hz, 26.1–26.2 °C), *L. oshanensis* (4402–4633 Hz, 14°C; recorded from c. 40 km from type locality of *L. oshanensis*), *L. solus* (3100–3200 Hz, 24.2–24.3°C), and *L. tuberosus* (2584–2756.2 Hz, 22.5–24.5 °C). Although frequency can vary with temperature, differences among species of the scale reported here are extremely unlikely to be attributed to temperature differences.

*Leptotalax aereus* is morphologically most similar to *L. oshanensis*, but differs from it by its call (above), and by lacking a distinct black line under the supratympanic fold and distinct black inter-orbital blotches that abut the inner margins of the orbital bulge (present in all *L. oshanensis* examined). *Leptotalax aereus* is also grey in preservative (compared to brown for *L. oshanensis*). Male *L. aereus* and male *L. oshanensis* do not differ in SVL (male *L. aereus* mean SVL  $27.3 \pm 0.9$  S. D., male *L. oshanensis* mean SVL  $27.2 \pm 0.7$  S. D.; Mann-Whitney *U*-test,  $Z = -0.641$ ,  $p = 0.522$ ;  $N = 42$ ), but *L. aereus* males have a greater head length (male *L. aereus* mean HDL  $10.2 \text{ mm} \pm 0.4$  S. D., male *L. oshanensis* mean HDL  $9.7 \text{ mm} \pm 0.3$  S. D.; Mann-Whitney *U*-test,  $Z = -3.910$ ,  $p < 0.001$ ;  $N = 42$ ), shorter snout length (male *L. aereus* mean SNT  $3.8 \text{ mm} \pm 0.2$  S. D., male *L. oshanensis* mean SNT  $4.0 \text{ mm} \pm 0.2$  S. D.; Mann-Whitney *U*-test,  $Z = 2.069$ ,  $p = 0.039$ ;  $N = 42$ ), and greater tibia length (male *L. aereus* mean TIB  $13.7 \text{ mm} \pm 0.5$  S. D., male *L. oshanensis* mean TIB  $13.2 \text{ mm} \pm 0.4$  S. D.; Mann-Whitney *U*-test,  $Z = -3.216$ ,  $p = 0.001$ ;  $N = 42$ ) than *L. oshanensis*.

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### Appendix 1. Comparative material examined.

- Leptolalax applebyi*: Vietnam, Quang Nam Province, Song Thanh Proposed Nature Reserve (AMS R 171703–171707; 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 melicus*: Cambodia, Ratanakiri Province, Virachey National Park (MVZ 258074–258077, MVZ 258197–258199; type specimens)
- Leptolalax oshanensis*: China, Sichuan Province, Hongya Xian (FMNH 232907–232921; c. 50 km from type locality)
- Leptolalax tuberosus*: Vietnam, Quang Nam Province, Song Thanh Proposed Nature Reserve (AMS R 171714–171722)