

## THREE NEW SPECIES OF SPINULE-BEARING FROGS ALLIED TO *RANA MEGATYMPANUM* BAIN, LATHROP, MURPHY, ORLOV AND HO, 2003 FROM LAOS AND VIETNAM

BRYAN L. STUART<sup>1,2,4</sup> AND RAOUL H. BAIN<sup>3</sup>

<sup>1</sup>The Field Museum, Department of Zoology, Division of Amphibians and Reptiles,  
1400 S. Lake Shore Dr., Chicago, IL 60605-2496, USA

<sup>2</sup>University of Illinois at Chicago, Department of Biological Sciences, 845 W. Taylor,  
Chicago, IL 60607-7060, USA

<sup>3</sup>American Museum of Natural History, Center for Biodiversity and Conservation, and, Division of Zoology  
(Herpetology), Central Park West at 79th Street, New York, NY 10024, USA

**ABSTRACT:** Three new species of frogs allied to *Rana megatympanum* are described from Laos and Vietnam. One new species is from the Bolaven Plateau of southern Laos, a second is from central Laos and adjacent central Vietnam, and a third is from northern Laos. The three new species are distinguished from similar species by skin texture, the location of white spinules on the skin in males and females, spotting on the lips, body size, relative tympanum size, and unpigmented eggs.

**Key words:** Laos; New species; Ranidae; Vietnam

BOURRET (1942) remains the major work on frogs of the family Ranidae in Laos and Vietnam, but a recent surge in species discoveries and descriptions (e.g., Bain and Nguyen, 2004; Bain et al., 2003; Inger and Kottelat, 1998; Inger et al., 1999; Orlov et al., 2003; Stuart and Chan-ard, 2005; Stuart et al., 2005) has increased the number of ranid species in these two countries from 32 (Bourret, 1942) to approximately 59.

Taxonomic revision by Bain et al. (2003) of the ranid “cascade frogs” allied to *Rana livida* (Blyth, 1856) using molecular and morphological methods resulted in the resurrection of several junior synonyms of *R. livida*, and the description of six new species from Vietnam. One of these new species, *R. megatympanum*, was described from Nghe An and Tuyen Quang Provinces in northern Vietnam, and is characterized by having olive to brown shagreened skin on the dorsum, dorsolateral folds in males only, males much smaller than females, males with very large tympana, dark spotting on the lips, and unpigmented eggs (Bain et al., 2003). Here we describe three new species of cascade ranids that superficially resemble *R. megatympanum*, one from southern Laos, one from central Laos and adjacent central Vietnam, and one from extreme

northern Laos. These new species are highly divergent in mitochondrial DNA from each other and from *R. megatympanum* (B. L. Stuart, unpublished data), and differ morphologically primarily by the presence of white spinules on the skin in males and females, body size, and relative tympanum size. The three new species are described here on the basis of their diagnostic differences in morphology.

Recently, Bain and Nguyen (2004) described *R. tabaca* from Ha Giang Province in the extreme north of Vietnam as a new species that also closely resembles *R. megatympanum*. During the course of this work, we re-examined the type series of *R. megatympanum* and *R. tabaca*, and found that some measurements of the type series of *R. megatympanum* reported in the original description (Bain et al., 2003) are in error. Most notably, the ratio of tympanum to eye diameter in paratype males of *R. megatympanum* is 0.51–0.70, not 0.96–1.54 as reported in Bain et al. (2003). This character served as the primary justification for distinguishing *R. tabaca* from *R. megatympanum*. With this correction, *R. tabaca* differs from *R. megatympanum* only by having the movable flap of skin on the outer edge of the fifth toe extending further on the metatarsus and by having males with very slightly larger snout-vent lengths. We view these remaining differences as minor (i.e., geographic variation), and consequently treat *R. tabaca*

<sup>4</sup> CORRESPONDENCE: e-mail, bstuart@fieldmuseum.org

TABLE 1.—Measurements (mm) of *Rana megatympnum* Bain, Lathrop, Murphy, Orlov and Ho, 2003, including the type series of its junior synonym, *Rana tabaca* Bain and Nguyen, 2004. Abbreviations defined in Materials and Methods.

Measurement	Adult female holotype	Adult males (paratypes and <i>tabaca</i> )	Adult females (holotype, paratypes, and <i>tabaca</i> )
	( <i>n</i> = 1)	Range; Mean $\pm$ SD ( <i>n</i> = 17)	Range; Mean $\pm$ SD ( <i>n</i> = 13)
SVL	99.6	49.4–61.1; 55.4 $\pm$ 3.6	89.2–106.5; 100.4 $\pm$ 4.9
HDL	38.8	20.5–24.9; 23.3 $\pm$ 1.3	32.9–42.4; 38.2 $\pm$ 3.2
HDW	33.8	17.3–20.8; 19.3 $\pm$ 0.9	31.3–36.2; 34.2 $\pm$ 1.6
SNT	17.4	8.1–10.1; 9.4 $\pm$ 0.6	14.3–17.7; 16.3 $\pm$ 1.2
EYE	10.6	6.3–8.4; 7.6 $\pm$ 0.6	9.6–13.8; 10.9 $\pm$ 1.1
IOD	9.0	4.3–5.8; 5.0 $\pm$ 0.5	8.4–11.5; 9.6 $\pm$ 0.8
TMP	4.5	4.0–5.3; 4.8 $\pm$ 0.4	4.2–5.7; 5.1 $\pm$ 0.4
TEY	4.4	1.2–1.9; 1.5 $\pm$ 0.2	3.3–4.6; 4.1 $\pm$ 0.4
TIB	65.8	30.7–39.2; 35.6 $\pm$ 1.9	60.9–69.1; 65.9 $\pm$ 2.3
FEM	55.4	25.1–33.1; 30.7 $\pm$ 2.0	51.9–63.6; 57.2 $\pm$ 3.7
HND	25.7	14.9–18.0; 16.6 $\pm$ 1.0	24.9–28.9; 26.8 $\pm$ 1.4
FTL	55.9	27.5–34.2; 30.9 $\pm$ 1.8	51.4–60.6; 56.2 $\pm$ 2.4
	( <i>n</i> = 1)	Range; Median ( <i>n</i> = 17)	Range; Median ( <i>n</i> = 13)
HDL:HDW	1.15	1.10–1.30; 1.21	1.00–1.18; 1.13
SNT:HDL	0.45	0.37–0.42; 0.40	0.40–0.46; 0.42
TMP:EYE	0.42	0.51–0.72; 0.63	0.41–0.56; 0.47
EYE:SNT	0.61	0.67–0.91; 0.81	0.59–0.79; 0.65
TIB:SVL	0.66	0.61–0.70; 0.64	0.63–0.69; 0.66

as a junior synonym of *R. megatympnum*. Therefore, our reference to *R. megatympnum* in this paper represents a composite of *R. megatympnum* and *R. tabaca* (Table 1).

#### MATERIALS AND METHODS

Specimens were caught by hand, euthanized in the field by immersion in a dilute chloretone solution, preserved in 10% buffered formalin, and later transferred to 70% ethanol. Tissue samples were taken from some individuals by preserving pieces of liver or muscle in 95% ethanol before the specimen was fixed in formalin. Specimens were deposited and comparative material was examined in the American Museum of Natural History (AMNH) and the Field Museum of Natural History (FMNH). Comparative material also was examined in the holdings of the California Academy of Sciences (CAS), the Royal Ontario Museum (ROM), The Natural History Museum, London (BMNH), and the University of California Museum of Vertebrate Zoology (MVZ).

Measurements (in mm) were made with dial calipers to the nearest 0.1 mm. Abbreviations used are: SVL = snout–vent length; HDL = head length from tip of snout to rear of the jaws; HDW = maximum head width; SNT =

snout length from tip of snout to the anterior corner of the eye; EYE = horizontal diameter of the exposed portion of the eyeball; IOD = interorbital distance at narrowest point; TMP = horizontal diameter of tympanum; TEY = distance from anterior edge of tympanum to posterior corner of the eye; TIB = tibia length; FEM = femur length, from vent to outer edge of knee; HND = hand length, from base of palm to tip of third finger; FTL = foot length, from proximal edge of inner metatarsal tubercle to tip of fourth toe.

In addition to the three new species presented here, 10 other ranid species from mainland Southeast Asia have the character combination of first finger longer than the second, digit tips expanded with circummarginal grooves, males with gular pouches, males without humeral glands, and females with unpigmented eggs: *Rana anlungensis* Liu and Hu in Hu et al., 1973, *R. banaorum* Bain, Lathrop, Murphy, Orlov and Ho, 2003, *R. chloronota* (Günther, 1875), *R. graminea* Boulenger, 1899, *R. hejiangensis* Deng and Yu, 1992, *R. livida* (Blyth, 1856), *R. megatympnum* Bain, Lathrop, Murphy, Orlov and Ho, 2003, *R. morafkai* Bain, Lathrop, Murphy, Orlov and Ho, 2003, *R. tiannanensis* (Yang and Li, 1980), and *R. trunkieni* Orlov et al., 2003. Currently, *Rana livida* sensu stricto is known

only from females (Bain et al., 2003) and *R. trunkieni* is known only from males (Orlov et al., 2003), but we conservatively list these two species because the relevant characteristics are exhibited by the known sexes. Likewise, the egg coloration is unknown in *R. hejiangensis*, but we conservatively list this species because it exhibits the remaining characteristics. The three new species described in this paper are compared against these ten species with which they can be most easily confused. Type specimens of all species except *R. tiannanensis* were examined (see Material Examined). Data for *R. tiannanensis* were taken from the original description (Yang and Li, 1980).

Higher-level taxonomy within the large family Ranidae remains problematic and uncertain (e.g., Dubois, 1992, 1999; Inger, 1996), largely due to a lack of phylogenetic studies to support classifications (Inger, 1996). The frogs allied to *R. livida* have been variously placed in the genera *Rana*, *Amolops*, *Huia*, *Hylarana*, and *Odorrana*, (Bain et al., 2003). We conservatively treat the three new species as members of the genus *Rana* sensu lato, pending phylogenetic study to support generic divisions.

#### SPECIES ACCOUNTS

##### *Rana bolavensis* sp. nov.

*Holotype*.—FMNH 258159 (field tag HKV 63794), adult male (Fig. 1), collected on a rock bank less than 1 m from a rocky stream in wet evergreen forest on the Bolaven Plateau in Dong Hua Sao National Biodiversity Conservation Area, Pakxong District, Champasak Province, Laos, near 15° 04' 37" N, 106° 08' 15" E, 1000 m elevation on 8 September 1999 by Bryan L. Stuart and Harold F. Heatwole.

*Paratypes*.—FMNH 258160–65, 258168, 258176, 258229–37, 258308–11 (21 males), FMNH 258588–91 (four females), FMNH 258166 (one juvenile), same data as holotype but collected 08–13 September 1999. FMNH 258167, 258242 (two males), FMNH 258241 (one juvenile), collected on the Bolaven Plateau, Dong Hua Sao National Biodiversity Conservation Area, near 15° 03' 55" N, 106° 13' 03" E, 1200 m elevation on 22–23 September 1999 by Bryan L. Stuart and Harold F. Heatwole.

*Diagnosis*.—A rapid frog having the following combination of characters: SVL 41.0–49.2 in males, 78.9–87.5 in females; TMP:EYE 0.52–0.67 in males, 0.37–0.46 in females; gular pouches in males; first finger longer than the second; all digit tips expanded with circum-marginal grooves; no outer metatarsal tubercle; skin on dorsum shagreened; glandular dorso-lateral fold in males, weakly visible or absent in females; white spinules on upper and lower parts in males, upper parts only in females; dark spots on lip; and unpigmented eggs.

*Rana bolavensis* differs from *R. anlungensis* by having larger SVL in both sexes (males 41.0–49.2, females 78.9–87.5 in *bolavensis*; males 34.5–38.4, females 59.6–67.2 in *anlungensis*) and having spinules on dorsum and venter (absent in *anlungensis*). *Rana bolavensis* differs from *R. banaorum* by having black spots on upper and lower lip (absent in *banaorum*), having males with spinules on venter (absent in *banaorum*), and having females with TMP:EYE 0.37–0.46 (0.63–0.87 in *banaorum*). *Rana bolavensis* differs from *R. chloronota* by having skin on dorsum shagreened (smooth in *chloronota*), having black spots on upper and lower lip (absent in *chloronota*), and having males with spinules on venter (absent in *chloronota*). *Rana bolavensis* differs from *R. graminea* by having skin on dorsum shagreened (smooth in *graminea*), having black spots on upper and lower lip (absent in *graminea*), and having spinules on dorsum and venter (absent in *graminea*). *Rana bolavensis* differs from *R. hejiangensis* by having skin on dorsum shagreened (smooth in *hejiangensis*), having spinules on dorsum and venter (absent in *hejiangensis*), and lacking distinct dark spots on chin and chest (present in *R. hejiangensis*). *Rana bolavensis* differs from *R. livida* by having skin on dorsum shagreened (smooth in *livida*), having black spots on upper and lower lip (absent in *livida*), and having the posterior surface of thigh brown with distinct yellowish-gray marbling (brown with distinct, whitish, round spots in *livida*). *Rana bolavensis* differs from *R. megalotypanum* by having spinules on dorsum and venter (absent in *megalotypanum*) and having smaller SVL in both sexes (males 41.0–49.2, females 78.9–87.5 in *bolavensis*; males 49.4–61.1, females 89.2–106.5 in *megalotypanum*). *Rana bolavensis* differs from *R. morafkai* by

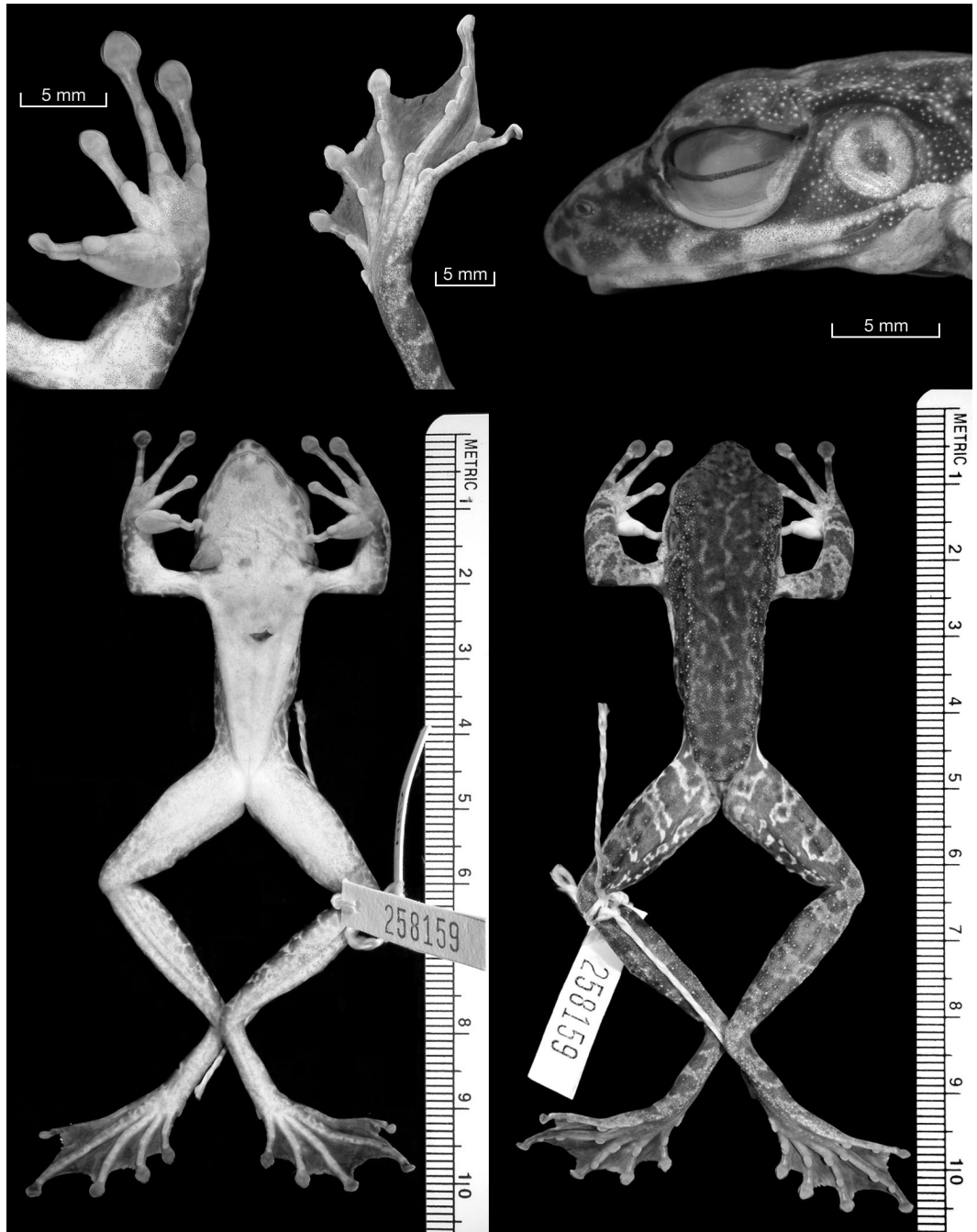


FIG. 1.—The adult male holotype (FMNH 258159) of *Rana bolavensis* sp. nov. in preservative (SVL 46.6).

having black spots on upper and lower lip (absent in *morafkai*), having males with spinules on venter (absent in *morafkai*), and having smaller TMP:EYE in both sexes (males

0.52–0.67, females 0.37–0.46 in *bolavensis*; males 0.78–1.27, females 0.53–1.07 in *morafkai*). *Rana bolavensis* differs from *R. tiannanensis* by having skin on dorsum

shagreened (rough, granular in *tiannanensis*), having spinules on dorsum and venter (absent in *tiannanensis*), having males with TMP:EYE 0.52–0.67 (0.72–0.76 in *tiannanensis*), having the dorsum dark brown with gray reticulations or dorsum uniformly dark blue-green (brownish-yellow in *tiannanensis*), and having the venter cream with diffuse gray markings (immaculate in *tiannanensis*). *Rana bolavensis* differs from *R. trankieni* by having males with SVL 41.0–49.2 (76.1–77.0 in *trankieni*), lacking a narrow, strongly protruding snout (present in *trankieni*), and having skin on dorsum shagreened (smooth in *trankieni*).

*Description of holotype*.—Habitus moderately slender; head narrow, longer than wide; snout obtusely pointed in dorsal view, projecting beyond lower jaw, round in profile, not depressed; nostril lateral, slightly closer to tip of snout than eye; canthus distinct, slightly constricted behind nostrils; lores concave and oblique; eye diameter about equal to snout length; interorbital distance less than width of upper eyelid; pineal body visible; tympanum distinct, round, 60% eye diameter, not depressed relative to skin of temporal region, tympanic rim elevated relative to tympanum; vomerine teeth on two oblique ridges, closer to each other than to choanae; tongue cordiform, deeply notched posteriorly, free for approximately two-thirds its length; vocal sac opening at corner of mouth; sac-like gular pouch at corner of throat.

Tips of all four fingers expanded with circummarginal grooves; width of Finger III disc about 2 times width of phalanx, about half the diameter of tympanum; relative finger lengths  $II < I < IV < III$ ; ventral callous pad on Fingers II, III, and IV from distal edge of proximal subarticular tubercle to base of disc; movable flap of skin on preaxial side of Fingers II and III; one subarticular tubercle on Fingers I and II, two subarticular tubercles on Fingers III and IV; one supernumerary tubercle proximal to proximal subarticular tubercle on Fingers II, III, and IV, smaller on II; two palmar tubercles, large, oval, in contact; velvety nuptial pad on Finger I, covering the dorsal surface to the level of the distal edge of the subarticular tubercle, covering the medial surface to base of finger disc with distinct constriction at the level of the distal edge of the subarticular tubercle; forearm robust.

Tips of toes expanded, width of Toe IV disc about equal to width of Finger III disc; Toe III shorter than Toe V; Toes I, II, III, and V fully webbed to base of discs; Toe IV fully webbed to distal subarticular tubercle with narrow extension to base of disc; movable flap of skin on preaxial side of Toe I from subarticular tubercle to base of disc, on postaxial side of Toe V from proximal edge of proximal subarticular tubercle to base of disc; elongate, oval inner metatarsal tubercle; no outer metatarsal tubercle.

Skin shagreened on dorsum; skin smooth on limbs, posterior half of flank, and venter; skin granular on anterior half of flank and posterior surface of thigh near vent; humeral gland absent; two rictal glands, anterior gland continuous with upper lip; glandular supratympanic fold present, continuing onto body as glandular dorsolateral fold, extending to near vent; white spinules on side and top of head, upper lip, upper eyelid, back, elbow, flank, underside of lower jaw, chest, and anterior half of belly; larger white spinules on loreal region, rictal region, tympanic region, posterior corner of upper eyelid, supratympanic fold, dorsolateral fold, sacral region just anterior to vent, dorsomedial surface of posterior half of thigh, dorsal surface of calf, and from heel to outer edge of Toe V.

Measurements of holotype (mm): SVL 46.6; HDL 18.5; HDW 15.0; SNT 7.0; EYE 6.4; IOD 4.1; TMP 3.8; TEY 1.3; TIB 27.8; FEM 20.6; HND 14.7; FTL 22.9.

*Color of holotype in preservative*.—Dorsum dark brown with gray reticulations; side of head, supratympanic fold, and dorsolateral fold black; upper and lower lip yellowish-gray with elongate black spots; nuptial pad and rictal glands creamy-white; flank whitish-gray with large, round black spots; forelimbs and dorsal surface of thigh light brown with dark brown marbling and crossbars; dorsal surface of calf and tarsus brown with dark brown crossbars; posterior surface of thigh and inguinal region brown with distinct yellowish-gray marbling; venter and ventral surface of forelimbs cream with diffuse gray markings; black axillary spot posterior to gular pouch; ventral surface of hindlimbs with grayish-brown mottling; toe webbing gray.

*Variation*.—Measurements of types summarized in Table 2. SVL of adult males

TABLE 2.—Measurements (mm) of *Rana bolavensis* sp. nov. Abbreviations defined in Materials and Methods.

Measurement	Adult males (holotype and paratypes)	Adult females (paratypes)
	Range; Mean $\pm$ SD ( $n = 24$ )	Range; Mean $\pm$ SD ( $n = 4$ )
SVL	41.0–49.2; 45.6 $\pm$ 2.4	78.9–87.5; 83.3 $\pm$ 3.6
HDL	16.1–19.7; 18.2 $\pm$ 1.1	29.3–34.1; 31.3 $\pm$ 2.0
HDW	12.9–15.7; 14.6 $\pm$ 0.7	25.8–29.4; 27.6 $\pm$ 1.5
SNT	6.3–7.7; 7.1 $\pm$ 0.4	12.6–14.3; 13.4 $\pm$ 0.8
EYE	5.2–6.8; 6.1 $\pm$ 0.5	9.3–10.9; 10.3 $\pm$ 0.8
IOD	3.3–4.6; 3.9 $\pm$ 0.3	5.7–7.4; 6.6 $\pm$ 0.8
TMP	3.0–4.0; 3.6 $\pm$ 0.3	4.0–5.0; 4.3 $\pm$ 0.5
TEY	0.9–1.8; 1.4 $\pm$ 0.2	3.8–4.2; 3.9 $\pm$ 0.2
TIB	25.2–29.2; 27.6 $\pm$ 1.1	52.9–58.6; 56.1 $\pm$ 2.9
FEM	20.4–24.2; 22.0 $\pm$ 1.0	39.6–45.9; 43.2 $\pm$ 2.7
HND	12.4–15.2; 13.8 $\pm$ 0.8	22.5–26.6; 24.6 $\pm$ 2.0
FTL	22.2–26.9; 24.3 $\pm$ 1.2	41.4–49.3; 46.1 $\pm$ 3.6
	Range; Median ( $n = 24$ )	Range; Median ( $n = 4$ )
HDL:HDW	1.07–1.34; 1.25	1.12–1.16; 1.13
SNT:HDL	0.35–0.45; 0.39	0.42–0.45; 0.43
TMP:EYE	0.52–0.67; 0.58	0.37–0.46; 0.42
EYE:SNT	0.70–0.97; 0.86	0.72–0.79; 0.77
TIB:SVL	0.57–0.64; 0.60	0.66–0.69; 0.67

47–62% SVL of adult females; tympanum of males relatively larger than tympanum of females (Table 2). Gular pouches appearing as wrinkled skin folds at corners of throat in three male paratypes. Ova in preservative uniformly yellow, without pigmented hemisphere, approximately 3 mm diameter. Dorsolateral fold weakly visible or absent in female paratypes. Females with fewer, smaller spinules than males and without spinules on underparts. Dorsum color in preservative like holotype in 11 males and one female, uniformly dark blue-green in 12 males and three females. Color of venter in preservative like holotype in ten males and one female, more heavily mottled with gray-brown in nine males and two females, throat and chest dark brown in four males and one female. Foot webbing of females dark brown in preservative.

**Distribution and ecology.**—*Rana bolavensis* is currently known only from wet evergreen forest at 1000–1200 m elevation on the Bolaven Plateau of southern Laos (Fig. 2), a large, volcanic plateau isolated from the Annamite Mountain chain by the Xe Kong River Valley. Specimens were collected at night on rocks and vegetation along rocky streams, except FMNH 258310 (adult male) was found at night on a low tree branch about 100 m from a stream, FMNH 258166 (juvenile) was found at night on leaf

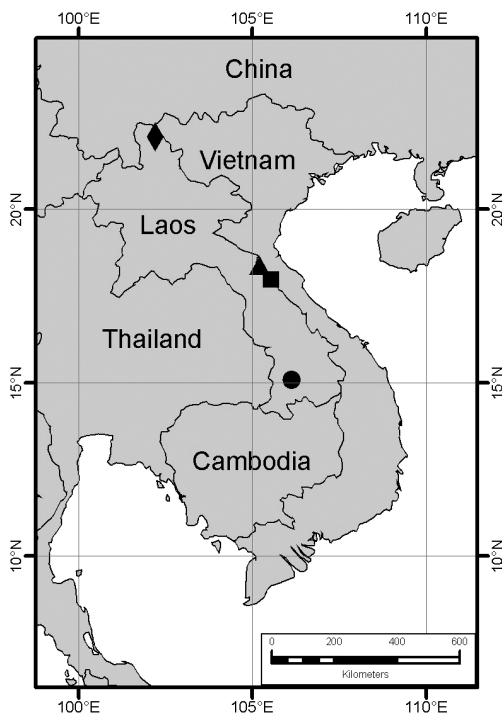


FIG. 2.—Map showing (circle) type locality of *Rana bolavensis* sp. nov., (square) type locality of *Rana orba* sp. nov., (triangle) Vietnam paratype locality of *Rana orba* sp. nov., and (diamond) type locality of *Rana heatwolei* sp. nov.

litter in the forest during a heavy rain, and FMNH 258241 (juvenile) was found during the day under leaf litter in the forest. These observations suggest that juveniles may be more terrestrial than adults. Many specimens of both sexes were infested with mites on the eyelid, fingers, and toe webbing. One other species of frog, *Leptobranchium buchari* Ohler, Teynié, and David, 2004, has been described from the highlands of the Bolaven Plateau, and may also be endemic to the area. Much of the wet evergreen forest on the top of the Bolaven Plateau is being converted to coffee plantations, a practice that probably threatens the survival of *R. bolavensis*.

**Etymology.**—The specific epithet *bolavensis* refers to the type locality on the Bolaven Plateau.

#### *Rana orba* sp. nov.

**Holotype.**—FMNH 256489 (field tag HKV 62824), adult male (Fig. 3), collected on a leaf of an herbaceous plant growing from a rock

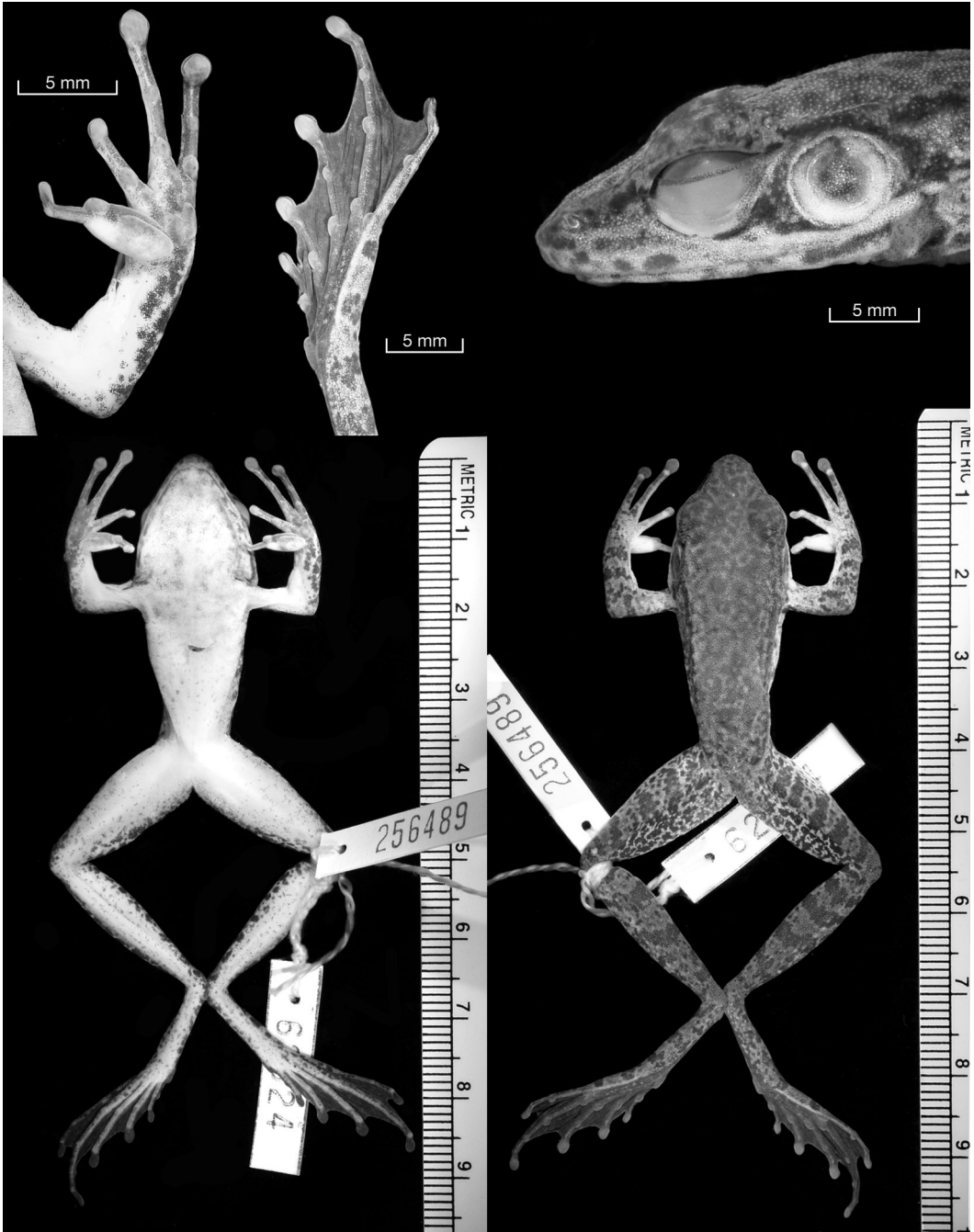


FIG. 3.—The adult male holotype (FMNH 256489) of *Rana orba* sp. nov. in preservative (SVL 40.5).

face 2 m above Houay Ting Tou Stream in evergreen forest in Nakai-Nam Theun National Biodiversity Conservation Area, Nakai District, Khammouan Province, Laos, 17° 58'

N, 105° 34' E, 700 m elevation on 9 November 1998 by Bryan L. Stuart.

*Paratypes*.—FMNH 256481–82, 256488 (three females), FMNH 256486–87 (two

immature females), same data as holotype but collected 7–9 November 1998. FMNH 256494 (one male), FMNH 256483 (one female), collected in Houay Duen Stream, Nakai-Nam Theun National Biodiversity Conservation Area, Nakai District, Khammouan Province, Laos, 17° 57' N, 105° 34' E, 700 m elevation on 10–12 November 1998 by Bryan L. Stuart. FMNH 256484 (one female), collected in Houay Balong Stream, Nakai-Nam Theun National Biodiversity Conservation Area, Nakai District, Khammouan Province, Laos, 17° 56' N, 105° 34' E, 600 m elevation on 16 November 1998 by Bryan L. Stuart. FMNH 256485 (one female), collected in Houay Dreng Stream, Nakai-Nam Theun National Biodiversity Conservation Area, Nakai District, Khammouan Province, Laos, 17° 56' N, 105° 34' E, 600 m elevation on 5 December 1998 by Bryan L. Stuart. FMNH 256490 (one female), collected in Houay Mae Stream, Nakai-Nam Theun National Biodiversity Conservation Area, Nakai District, Khammouan Province, Laos, 17° 57' N, 105° 35' E, 600 m elevation on 13 November 1998 by Bryan L. Stuart. FMNH 258132, 258153, 258155 (three males), collected in the Nape border area, Khamkeut District, Bolikhamxay Province, Laos, near 18° 18' N, 105° 04' E on 15–17 March 1997 by David Davenport. AMNH 161251 (one juvenile), collected in tributary of Rao An River, Rao An region, Huong Son Reserve, Huong Son District, Ha Tinh Province, Vietnam, 18° 21' 53" N, 105° 13' 13" E, 200 m elevation on 11 May 1998 by David A. Kizirian.

*Diagnosis.*—A ranid frog having the following combination of characters: SVL 37.3–41.3 in males, 76.8–94.0 in females; TMP:EYE 0.62–0.72 in males, 0.45–0.55 in females; gular pouches in males; first finger longer than the second; all digit tips expanded with circum-marginal grooves; no outer metatarsal tubercle; skin on dorsum heavily shagreened; glandular dorsolateral fold in males, weakly visible in females; white spinules on upper and lower parts in males, absent in females; dark spots on lip; and unpigmented eggs.

*Rana orba* differs from *R. anlungensis* by having females with SVL 76.8–94.0 (59.6–67.2 in *anlungensis*) and having males with spinules on dorsum and venter (absent in *anlungensis*). *Rana orba* differs from *R. banaorum* by having

skin on dorsum heavily shagreened with some large tubercles (smooth or shagreened in *banaorum*), having brown spots on upper and lower lip (absent in *banaorum*), having males with spinules on venter (absent in *banaorum*), having males with SVL 37.3–41.3 (42.5–54.6 in *banaorum*), and having females with TMP:EYE 0.45–0.55 (0.63–0.87 in *banaorum*). *Rana orba* differs from *R. bolavensis* by having skin on dorsum heavily shagreened with some large tubercles (shagreened in *bolavensis*), having males with SVL 37.3–41.3 (41.0–49.2 in *bolavensis*), having females without spinules (present on upperparts in *bolavensis*), and having females with TMP:EYE 0.45–0.55 (0.37–0.46 in *bolavensis*). *Rana orba* differs from *R. chloronota* by having skin on dorsum heavily shagreened with some large tubercles (smooth in *chloronota*), having black spots on upper and lower lip (absent in *chloronota*), and having males with spinules on venter (absent in *chloronota*). *Rana orba* differs from *R. graminea* by having skin on dorsum heavily shagreened with some large tubercles (smooth in *graminea*), having black spots on upper and lower lip (absent in *graminea*), and having males with spinules on dorsum and venter (absent in *graminea*). *Rana orba* differs from *R. hejiangensis* by having males with SVL 37.3–41.3 (44–56 in *hejiangensis*), having skin on dorsum heavily shagreened with some large tubercles (smooth in *hejiangensis*), having males with spinules on dorsum and venter (absent in *hejiangensis*), and lacking distinct dark spots on chin and chest (present in *R. hejiangensis*). *Rana orba* differs from *R. livida* by having skin on dorsum heavily shagreened with some large tubercles (smooth in *livida*), having black spots on upper and lower lip (absent in *livida*), and having the posterior surface of thigh creamy-white with marbled black reticulations (brown with distinct, whitish, round spots in *livida*). *Rana orba* differs from *R. megatympanum* by having skin on dorsum heavily shagreened with some large tubercles (shagreened in *megatympanum*), having males with spinules on dorsum and venter (absent in *megatympanum*), and having males with SVL 37.3–41.3 (49.4–61.1 in *megatympanum*). *Rana orba* differs from *R. morafkai* by having skin on dorsum heavily shagreened with some large tubercles (smooth or shagreened in *morafkai*), having black spots

on upper and lower lip (absent in *morafkai*), having males with spinules on the venter (absent in *morafkai*), and having males with TMP: EYE 0.62–0.72 (0.78–1.27 in *morafkai*). *Rana orba* differs from *R. tiannanensis* by having males with spinules on dorsum and venter (absent in *tiannanensis*) and having males with SVL 37.3–41.3 (52.5–53.5 in *tiannanensis*). *Rana orba* differs from *R. trankieni* by having males with SVL 37.3–41.3 (76.1–77.0 in *trankieni*), lacking a narrow, strongly protruding snout (present in *trankieni*), and having skin on dorsum heavily shagreened with some large tubercles (smooth in *trankieni*).

*Description of holotype*.—Habitus moderately slender; head narrow, longer than wide; snout obtusely pointed in dorsal view, projecting beyond lower jaw, round in profile, not depressed; nostril lateral, closer to tip of snout than eye; canthus distinct, slightly constricted behind nostrils; lores concave and oblique; eye diameter about equal to snout length; interorbital distance less than width of upper eyelid; pineal body visible; tympanum distinct, round, 67% eye diameter, not depressed relative to skin of temporal region, tympanic rim elevated relative to tympanum; vomerine teeth on two slightly oblique ridges, closer to each other than to choanae; tongue cordiform, deeply notched posteriorly, free for approximately two-thirds its length; vocal sac opening at corner of mouth; gular pouch appearing as wrinkled skin fold at corner of throat.

Tips of all four fingers expanded with circummarginal grooves; width of Finger III disc about 1.5 times width of phalanx, 37% diameter of tympanum; relative finger lengths  $II < I < IV < III$ ; ventral callous pad on Fingers II, III, and IV from distal edge of proximal subarticular tubercle to base of disc; movable flap of skin on preaxial side of Fingers II and III; one subarticular tubercle on Fingers I and II, two subarticular tubercles on Fingers III and IV; one supernumerary tubercle proximal to proximal subarticular tubercle on Fingers II, III, and IV; two palmar tubercles, oval, in contact; velvety nuptial pad on Finger I, covering the dorsal surface to the level of the subarticular tubercle, covering the medial surface to base of finger disc with distinct constriction at the level of the distal edge of the subarticular tubercle; forearm moderately robust.

Tips of toes expanded, width of Toe IV disc smaller than width of Finger III disc; Toe III shorter than Toe V; Toes I, II, III, and V fully webbed to base of discs; Toe IV fully webbed to between distal subarticular tubercle and base of disc, with narrow extension to base of disc; movable flap of skin on preaxial side of Toe I from subarticular tubercle to base of disc, on postaxial side of Toe V from slightly proximal of proximal subarticular tubercle to base of disc; elongate, oval inner metatarsal tubercle; no outer metatarsal tubercle.

Skin heavily shagreened with some large tubercles on dorsum; skin heavily shagreened on temporal region, loreal region, and dorsal surface of calf; skin shagreened on dorsal surface of thigh and ventral surface of feet; skin smooth on forelimb, venter, anterior surface of thigh, ventral surface of calf, and dorsal surface of feet; skin with large, elongated tubercles on flank; skin granular on posterior surface of thigh, continuing to posterior-ventral surface of thigh; humeral gland absent; two rictal glands, anterior gland continuous with upper lip; glandular supratympanic fold present, continuing onto body as glandular dorsolateral fold, extending to near vent; white spinules on top of head, posterior corner of upper eyelid, dorsum, chest, underside of lower jaw, and anterior one-fourth of belly.

Measurements of holotype: SVL 40.5; HDL 17.2; HDW 13.9; SNT 6.8; EYE 6.1; IOD 3.8; TMP 4.1; TEY 1.2; TIB 26.3; FEM 21.1; HND 12.6; FTL 22.7.

*Color of holotype in preservative*.—Dorsum from top of head to sacrum gray-blue, sacrum brown, all with small brown reticulations; loreal region brown, temporal and tympanic region black; upper and lower lip gray with brown spotting; nuptial pad and rictal gland creamy-white; flank gray-brown with dark brown spots, near groin white with few dark spots, some creamy-white tubercles; limbs brown with dark brown crossbars; anterior surface of thigh brown with dark brown spots, posterior surface of thigh creamy-white with marbled black reticulations; venter cream with diffuse gray markings except immaculate on ventral surface of thigh near vent; black axillary spot posterior to gular pouch; toe webbing brown.

*Variation*.—Measurements of types summarized in Table 3. SVL of adult males

TABLE 3.—Measurements (mm) of *Rana orba* sp. nov. Abbreviations defined in Materials and Methods.

Measurement	Adult males (holotype and paratypes)	Adult females (paratypes)
	Range; Mean $\pm$ SD ( $n = 5$ )	Range; Mean $\pm$ SD ( $n = 7$ )
SVL	37.3–41.3; 39.9 $\pm$ 1.5	76.8–94.0; 85.0 $\pm$ 6.7
HDL	15.9–18.2; 17.2 $\pm$ 0.8	29.9–36.3; 33.5 $\pm$ 2.4
HDW	13.1–14.8; 14.1 $\pm$ 0.6	25.5–31.3; 28.4 $\pm$ 2.5
SNT	6.4–7.1; 6.7 $\pm$ 0.3	11.9–15.6; 13.8 $\pm$ 1.4
EYE	5.3–6.6; 5.8 $\pm$ 0.5	10.1–11.4; 10.9 $\pm$ 0.5
IOD	3.5–4.2; 3.7 $\pm$ 0.3	6.0–8.4; 7.0 $\pm$ 0.9
TMP	3.8–4.1; 3.9 $\pm$ 0.1	4.7–6.3; 5.3 $\pm$ 0.5
TEY	0.7–1.2; 1.0 $\pm$ 0.2	2.4–4.2; 3.1 $\pm$ 0.6
TIB	23.4–27.3; 26.0 $\pm$ 1.6	52.9–62.2; 57.3 $\pm$ 3.9
FEM	19.4–23.5; 21.4 $\pm$ 1.8	41.5–51.0; 45.4 $\pm$ 3.7
HND	11.5–13.0; 12.4 $\pm$ 0.6	21.9–27.3; 24.4 $\pm$ 2.2
FTL	19.8–22.9; 22.0 $\pm$ 1.3	41.9–53.1; 46.7 $\pm$ 4.2
	Range; Median ( $n = 5$ )	Range; Median ( $n = 7$ )
HDL:HDW	1.17–1.26; 1.22	1.16–1.23; 1.17
SNT:HDL	0.37–0.43; 0.39	0.39–0.42; 0.40
TMP:EYE	0.62–0.72; 0.70	0.45–0.55; 0.48
EYE:SNT	0.78–0.92; 0.85	0.78–0.88; 0.80
TIB:SVL	0.63–0.68; 0.65	0.65–0.70; 0.68

40–54% SVL of adult females; tympanum of males relatively larger than tympanum of females (Table 3). Ova in preservative uniformly yellow, without pigmented hemisphere, approximately 2.0–2.5 mm diameter. Dorsolateral fold in immature females as in holotype, in adult females and one adult male paratype only weakly visible. Large tubercles on flank low, weakly visible in three male paratypes. Some male paratypes with sac-like gular pouches. No white spinules in females. Dorsum in preservative brown with small dark brown reticulations in seven adult females, brown with small dark brown spots in one adult female. Venter in preservative of both sexes variable in amount of diffuse gray markings, but ventral surface of thigh near vent always immaculate.

*Distribution and ecology.*—*Rana orba* is currently known from the northern Truong Son (Annamite Highlands) of the Laos-Vietnam frontier in eastern Khammouan and Bolikhamxay Provinces, Laos, and western Ha Tinh Province, Vietnam (Fig. 2). Specimens were collected at night in evergreen forest on leaf litter, rocks, rock ledges, logs, tree roots, and vegetation within 6 m of rocky streams. The Laos specimens were found at 600–700 m elevation and the single Vietnam specimen was found at 200 m elevation.

*Etymology.*—The specific epithet *orba* (L.) for orphan, is in reference to the species being known in Vietnam only from a single juvenile.

#### *Rana heatwolei* sp. nov.

*Holotype.*—FMNH 258134 (field tag HKV 64206), adult male (Fig. 4), collected on a tree root projecting from a dirt bank 2 m above a tributary of the Nam Ou River in evergreen forest in Phou Dendin National Biodiversity Conservation Area, Phongsaly District, Phongsaly Province, Laos, 22° 5' 38" N, 102° 12' 50" E, 600 m elevation, 7 October 1999 by Bryan L. Stuart and Harold F. Heatwole.

*Paratypes.*—FMNH 258279, 258598 (two females), same data as holotype. FMNH 258135 (one male), FMNH 258280 (one female), same data as holotype except collected 08 October 1999. FMNH 258136–37 (two males), collected near Nam Khang River, Phou Dendin National Biodiversity Conservation Area, Phongsaly District, Phongsaly Province, Laos, near 22° 09' 04" N, 102° 12' 19" E, 600 m elevation on 12–14 October 1999 by Bryan L. Stuart and Harold F. Heatwole. FMNH 258138 (one male), collected in Houay Han Stream near Nam Ou River, Phou Dendin National Biodiversity Conservation Area, Phongsaly District, Phongsaly Province, Laos, near 22° 05' 31" N, 102° 06' 19" E, 600–800 m elevation on 19 October 1999 by Bryan L. Stuart and Harold F. Heatwole. FMNH 258139 (one male), FMNH 258282–83 (two females), FMNH 258281 (one immature female), collected in Houay Aw Stream near Nam Ou River, Phou Dendin National Biodiversity Conservation Area, Phongsaly District, Phongsaly Province, Laos, near 22° 05' 44" N, 102° 08' 10" E, 600–800 m elevation on 23–24 October 1999 by Bryan L. Stuart and Harold F. Heatwole.

*Diagnosis.*—A rapid frog having the following combination of characters: SVL 37.1–57.3 in males, 97.3–103.8 in females; TMP:EYE 0.58–0.69 in males, 0.45–0.50 in females; gular pouches in males; first finger longer than the second; all digit tips expanded with circum-marginal grooves; skin on dorsum shagreened; glandular dorsolateral fold in males, absent in females; white spinules on upper and lower parts in males, absent in females; dark spots on lip; and unpigmented eggs.

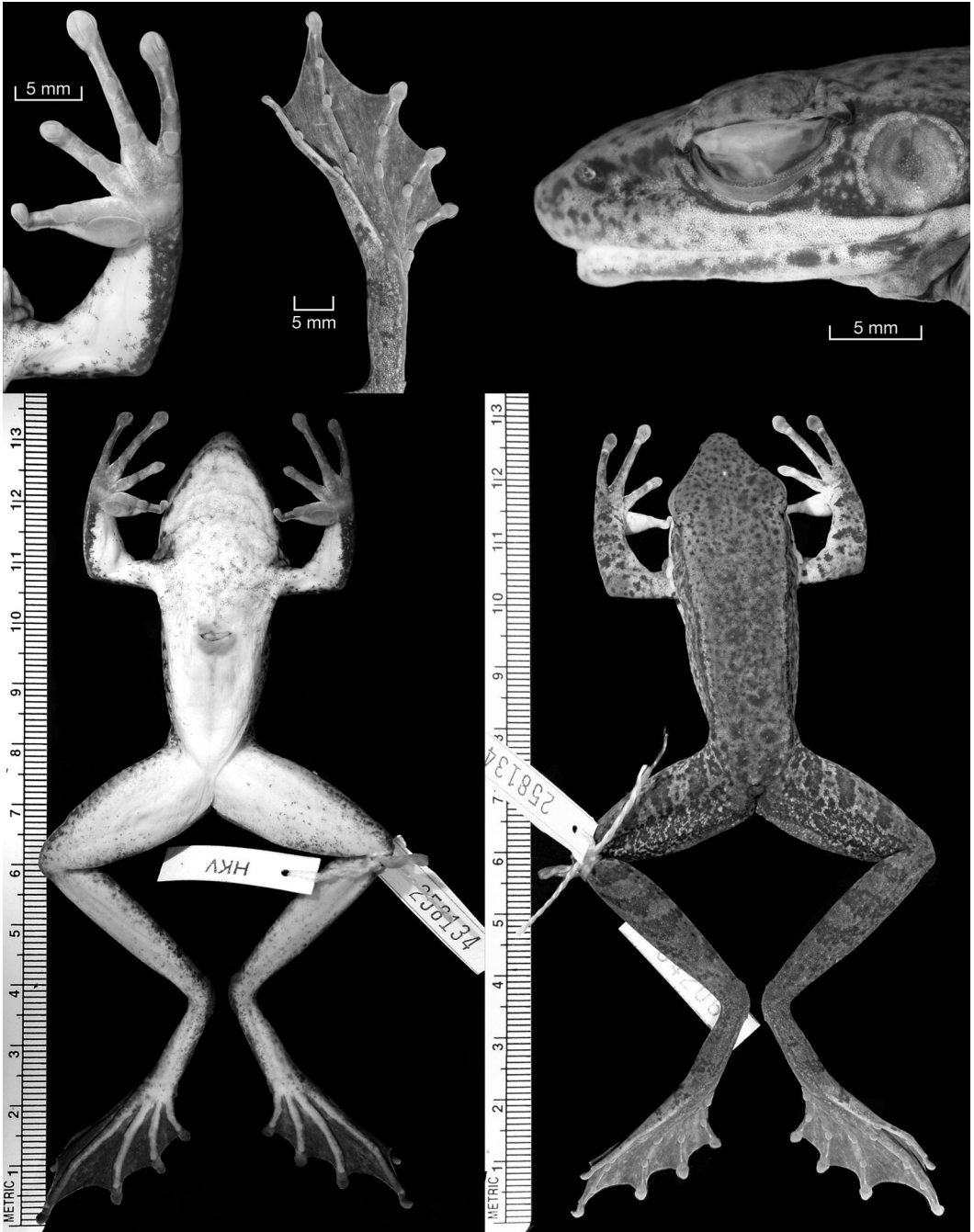


FIG. 4.—The adult male holotype (FMNH 258134) of *Rana heatwolei* sp. nov in preservative (SVL 57.3).

*Rana heatwolei* differs from *R. anlungensis* by having females with SVL 97.3–103.8 (59.6–67.2 in *anlungensis*) and having males with spinules on dorsum and venter (absent in

*anlungensis*). *Rana heatwolei* differs from *R. banaorum* by having brown spots on upper and lower lip (absent in *banaorum*), having males with spinules on venter (absent in *banaorum*),

having females with TMP:EYE 0.45–0.50 (0.63–0.87 in *banaorum*), and having the dorsum brown with distinct, small dark brown spots (large black spots, if present, in *banaorum*). *Rana heatwolei* differs from *R. bolavensis* by having the dorsum brown with distinct, small dark brown spots (absent in *bolavensis*), having females without spinules (present on upperparts in *bolavensis*), having females with SVL 97.3–103.8 (78.9–87.5 in *bolavensis*), and having females with TMP:EYE 0.45–0.50 (0.37–0.46 in *bolavensis*). *Rana heatwolei* differs from *R. chloronota* by having skin on dorsum shagreened (smooth in *chloronota*), having brown spots on upper and lower lip (absent in *chloronota*), and having males with spinules on venter (absent in *chloronota*). *Rana heatwolei* differs from *R. graminea* by having skin on dorsum shagreened (smooth in *graminea*), having brown spots on upper and lower lip (absent in *graminea*), and having males with spinules on dorsum and venter (absent in *graminea*). *Rana heatwolei* differs from *R. hejiangensis* by having females with SVL 97.3–103.8 (86 in *hejiangensis*), having skin on dorsum shagreened (smooth in *hejiangensis*), having males with spinules on dorsum and venter (absent in *hejiangensis*), and lacking distinct dark spots on chin and chest (present in *R. hejiangensis*). *Rana heatwolei* differs from *R. livida* by having skin on dorsum shagreened (smooth in *livida*), having brown spots on upper and lower lip (absent in *livida*), and having the posterior surface of thigh gray with marbled black reticulations (brown with distinct, whitish, round spots in *livida*). *Rana heatwolei* differs from *R. megatympanum* by having males with spinules on dorsum and venter (absent in *megatympanum*) and having dorsum with distinct, small dark brown spots (absent in *megatympanum*). *Rana heatwolei* differs from *R. morafkai* by having brown spots on upper and lower lip (absent in *morafkai*), having males with spinules on venter (absent in *morafkai*), and having smaller TMP:EYE in both sexes (males 0.58–0.69, females 0.45–0.50 in *heatwolei*; males 0.78–1.27, females 0.53–1.07 in *morafkai*). *Rana heatwolei* differs from *R. orba* by having skin on dorsum shagreened (skin on dorsum heavily shagreened with some large tubercles in *orba*) and females with SVL 97.3–103.8 (76.8–94.0 in *orba*). *Rana heatwolei* differs from *R. tiannanensis* by having skin

on dorsum shagreened (rough, granular in *tiannanensis*), having males with spinules on dorsum and venter (absent in *tiannanensis*), and having the venter cream with diffuse brown markings except immaculate on posterior two-thirds of belly and ventral surface of thigh near vent (immaculate throughout in *tiannanensis*). *Rana heatwolei* differs from *R. trankieni* by having males with SVL 37.1–57.3 (76.1–77.0 in *trankieni*), lacking a narrow, strongly protruding snout (present in *trankieni*), and having skin on dorsum shagreened (smooth in *trankieni*).

*Description of holotype*.—Habitus moderately slender; head narrow, longer than wide; snout obtusely pointed in dorsal view, projecting beyond lower jaw, round in profile, not depressed; nostril lateral, closer to tip of snout than eye; canthus distinct, slightly constricted behind nostrils; lores concave and oblique; eye diameter about equal to snout length; interorbital distance less than width of upper eyelid; pineal body visible; tympanum distinct, round, 58% eye diameter, not depressed relative to skin of temporal region, tympanic rim elevated relative to tympanum, ventral margin of tympanic rim obscured by rear portion of upper lip; vomerine teeth on two transverse ridges closer to each other than to choanae; tongue cordiform, deeply notched posteriorly, free for approximately two-thirds its length; vocal sac opening at corner of mouth; sac-like gular pouch at corner of throat.

Tips of all four fingers expanded with circummarginal grooves; width of Finger III disc about 1.5 times width of phalanx, 45% diameter of tympanum; relative finger lengths  $II < I < IV < III$ ; ventral callous pad on Fingers II, III, and IV from distal edge of proximal subarticular tubercle to base of disc; movable flap of skin on preaxial side of Fingers II and III; one subarticular tubercle on Fingers I and II, two subarticular tubercles on Fingers III and IV; one supernumerary tubercle proximal to proximal subarticular tubercle on Fingers II, III, and IV; two palmar tubercles, large, oval, in contact; velvety nuptial pad on Finger I, covering the dorsal surface to the level of the subarticular tubercle, covering the medial surface to base of finger disc with distinct constriction at the level of

the distal edge of the subarticular tubercle; forearm robust.

Tips of toes expanded, width of Toe IV disc equal to width of Finger III disc; Toe III shorter than Toe V; Toes I, II, III, and V fully webbed to base of discs; Toe IV fully webbed to between distal subarticular tubercle and base of disc, with narrow extension to base of disc; movable flap of skin on preaxial side of Toe I from subarticular tubercle to base of disc, on postaxial side of Toe V from proximal edge of proximal subarticular tubercle to base of disc; elongate, oval inner metatarsal tubercle; outer metatarsal tubercle on right foot only.

Skin shagreened on dorsum, loreal region, and dorsal surface of calf; skin smooth on limbs and venter; skin heavily granular on flank; skin granular on posterior surface of thigh, continuing to posterior-ventral surface of thigh; humeral gland absent; two rictal glands, anterior gland continuous with upper lip; weakly visible glandular supratympanic fold from rear of eye to rear of tympanum, in contact with glandular dorsolateral fold extending to near vent; white spinules on dorsolateral fold, sacral region, underside of lower jaw, throat, chest, ventrolateral region of belly, in longitudinal row on dorsal surface of calf.

Measurements of holotype (mm): SVL 57.3; HDL 24.6; HDW 18.8; SNT 8.7; EYE 7.8; IOD 5.3; TMP 4.6; TEY 2.1; TIB 37.6; FEM 29.0; HND 17.6; FTL 32.2.

*Color of holotype in preservative.*—Dorsum and loreal region brown with distinct, small dark brown spots; temporal and tympanic region black, continuing as black streak below edge of dorsolateral fold; flank whitish-gray with black spots; nuptial pad creamy-white; limbs brown with dark brown crossbars and spots, posterior surface of thigh gray with marbled black reticulations; upper lip gray with brown spotting anterior to eye, creamy-white with diffuse gray markings posterior to eye, lower lip gray with brown spotting; rictal gland creamy-white with diffuse gray markings; venter cream with diffuse brown markings except immaculate on posterior two-thirds of belly and ventral surface of thigh near vent; black axillary spot posterior to gular pouch; toe webbing brown.

*Coloration of paratype female in life.*—Dorsum and loreal region reddish-brown with distinct, small black spots; temporal and



FIG. 5.—An adult female paratype of *Rana heatwolei* sp. nov. in life.

tympanic region black, continuing as black streak below edge of dorsolateral fold; upper half of flank brown, lower half of flank yellowish-brown, entire flank with dark brown and black spots; limbs brown with dark brown crossbars and spots; upper surface of fingers and toes yellowish; upper and lower lip yellow with gray and brown spotting; rictal gland yellow (Fig. 5).

*Variation.*—Measurements of types summarized in Table 4. SVL of males 36–59% SVL of females; tympanum of males relatively larger than tympanum of females (Table 4). Ventral margin of tympanic rim not obscured by rear portion of upper lip in adult females. Ova in preservative uniformly creamy-yellow, without pigmented hemisphere, approximately 2.0 mm diameter. Females and two males with interorbital distance greater than width of upper eyelid, two males with interorbital distance equal to width of upper eyelid. Females without dorsolateral fold and white spinules. Vomerine ridges slightly oblique in some paratypes. Outer metatarsal tubercle absent in paratypes, except weakly visible on right foot only of male FMNH 259139, as in holotype.

*Distribution and ecology.*—*Rana heatwolei* is currently known only from Phou Dendin National Biodiversity Conservation Area, Phongsaly Province, northern Laos, near the frontier with Vietnam and China (Fig. 2). Specimens were collected at night in hill evergreen forest at 600–800 m elevation on dirt banks, rocks, logs, tree roots, and vegetation within 4 m of rocky streams.

TABLE 4.—Measurements (mm) of *Rana heatwolei* sp. nov. Abbreviations defined in Materials and Methods.

Measurement	Adult males (holotype and paratypes)	Adult females (paratypes)
	Range; Mean $\pm$ SD ( $n = 6$ )	Range; Mean $\pm$ SD ( $n = 5$ )
SVL	37.1–57.3; 50.1 $\pm$ 6.9	97.3–103.8; 102.0 $\pm$ 2.7
HDL	16.9–24.6; 21.1 $\pm$ 2.5	37.7–40.2; 39.2 $\pm$ 1.0
HDW	12.5–18.8; 16.4 $\pm$ 2.1	31.7–35.6; 34.2 $\pm$ 1.5
SNT	6.4–8.7; 8.1 $\pm$ 0.9	16.5–18.0; 17.3 $\pm$ 0.6
EYE	4.6–7.8; 6.4 $\pm$ 1.0	10.3–11.7; 11.2 $\pm$ 0.6
IOD	3.4–5.3; 4.6 $\pm$ 0.7	10.2–11.1; 10.7 $\pm$ 0.3
TMP	3.2–4.6; 4.0 $\pm$ 0.5	5.1–5.4; 5.3 $\pm$ 0.1
TEY	0.8–2.1; 1.4 $\pm$ 0.4	3.8–5.0; 4.4 $\pm$ 0.5
TIB	23.4–37.6; 33.0 $\pm$ 5.2	64.7–69.7; 66.8 $\pm$ 2.1
FEM	20.0–29.0; 26.2 $\pm$ 3.3	60.4–64.8; 62.4 $\pm$ 1.7
HND	12.0–17.6; 15.9 $\pm$ 2.0	29.5–31.9; 30.7 $\pm$ 0.9
FTL	19.1–32.2; 28.0 $\pm$ 4.5	55.1–59.4; 57.0 $\pm$ 1.9
	Range; Median ( $n = 6$ )	Range; Median ( $n = 5$ )
HDL:HDW	1.24–1.36; 1.29	1.11–1.19; 1.14
SNT:HDL	0.35–0.41; 0.38	0.42–0.46; 0.44
TMP:EYE	0.58–0.69; 0.65	0.45–0.50; 0.47
EYE:SNT	0.73–0.90; 0.76	0.60–0.67; 0.66
TIB:SVL	0.63–0.71; 0.65	0.63–0.67; 0.65

*Etymology*.—The specific epithet is a patronym for Dr. Harold F. Heatwole, co-collector of the new species, whose guidance, support, and companionship greatly aided the senior author in conducting herpetological fieldwork in Laos.

#### DISCUSSION

Our descriptions of three additional species supplement the recent findings that the morphologically variable cascade ranids allied to *R. livida* represent a complex of species living in the montane lotic streams of Laos and Vietnam (Bain and Nguyen, 2004; Bain et al., 2003; Orlov et al., 2003; Stuart et al., 2005). Often more than one species in this complex occurs sympatrically, but only *R. chloronota* is currently recognized to be relatively widespread (Bain and Nguyen, 2004; Bain et al., 2003). The discovery of many new species with relatively small distributions has important consequences for conservation of biodiversity in Indochina. Further studies to identify evolutionary lineages in these frogs, and their phylogenetic relationships to each other, are warranted and underway (B. L. Stuart, unpublished data).

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- Rana bolavensis* (30).—Champasak Province, Laos: FMNH 258159, holotype male; FMNH 258160–65, 258167–68, 258176, 258229–37, 258242, 258308–11, paratype males; FMNH 258588–91, paratype females; FMNH 258166, 258241, paratype juveniles.
- Rana chloronota* (16).—Darjeeling, India: BMNH 1947.2.28.10, 1947.2.28.12, male syntypes; BMNH 1947.2.28.6 female syntype (note: BMNH catalog number correction from Bain et al., 2003, as per B. Clarke, personal communication). Assam, India: FMNH 72416, 74158, males. Shan State, Myanmar: CAS 221771–72, males. Rakhine State, Myanmar: CAS 220261, male; CAS 216574, 220186–87, 220260, 222907, females. Kachin State, Myanmar: CAS 221315, female. Bago State, Myanmar: CAS 211719, 211671, females.
- Rana graminea* (3).—Hainan Province, China: BMNH 1947.2.27.96–97, male syntypes; MVZ 230420, male.
- Rana heatwolei* (12).—Phongsaly Province, Laos: FMNH 258134, holotype male; FMNH 258135–39, paratype males; FMNH 258598, 258279–83, paratype females.
- Rana livida* (3).—Thagata Juwa, Dawna Mountains, Myanmar: BMNH 1889.3.25.48, female neotype; BMNH 1889.3.25.47, female. Prachuap Kirikhan Province, Thailand: FMNH 263415, female.
- Rana megalympanum* (25).—Nghe An Province, Vietnam: ROM 39684, female holotype; ROM 26398–400, 39263, 39685–39691, female paratypes; FMNH 255647–48, males; FMNH 255649, female. Tuyen Quang Province, Vietnam: ROM 39237–39240, paratype males. Lao Cai Province, Vietnam: AMNH 168747–48, 168751–52, males; AMNH 168741–42, females.
- Rana morafkai* (33).—Gia Lai Province, Vietnam: ROM 39932, female holotype; ROM 25094–97, 25099, 25101, 25104–06, 25108–11, 39904–11, 39937, paratype males; ROM 39930, 39934, 39947, 39949, paratype females. Champasak Province, Laos: FMNH 258238–40, males; FMNH 258592–94, females.
- Rana orba* (15).—Khammouan Province, Laos: FMNH 256489, holotype male; FMNH 256494, paratype male; FMNH 256481–87, 256488, 256490, paratype females. Bolikhamxay Province, Laos: FMNH 258132, 258153, 258155, paratype males. Ha Tinh Province, Vietnam: AMNH 161251, paratype juvenile.
- Rana tabaca* (10).—Ha Giang Province, Vietnam: AMNH 163923, male holotype; AMNH 163914–19, male paratypes; AMNH 163920–22, female paratypes.

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## APPENDIX I

### Specimens Examined

*Rana banaorum* (30).—Gia Lai Province, Vietnam: ROM 39944, holotype female; ROM 25084–86, 25100, 25102–03, 39716–20, 39912–13, 39915–16, 39920–22, 39924–26, paratype males; ROM 39899–901, 39928–29, 39931, 39936, 39941, paratype females.