Nomenclatural Status of the Synonyms of *Hyla pardalis* , and Taxonomic Position of *Hyla biobeba* (Anura: Hylidae)

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Taxonomy of Costa Rican Toads Referred to *Bufo melanochlorus* Cope, with the Description of a New Species

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ABSTRACT.—**We review the taxonomic status of populations of toads referred to *Bufo melanochlorus* Cope, 1877, that occur in the wet forests on both Atlantic and Pacific versants of Costa Rica. Populations from Pacific versant of Costa Rica and adjacent Panama are qualitatively diagnosable from all other populations and are described herein as a new species. The taxon *B. melanochlorus* is restricted to populations in the Atlantic and Montane Slopes and Cordillera Central faunal areas of Costa Rica.**

RESUMEN.—**Revisamos el estado taxonómico de las poblaciones de los sapos referidos a *Bufo melanochlorus* Cope, 1887. Estos ocurren en los bosques mésicos de la vertiente del Atlántico y la vertiente del Pacífico de Costa Rica y Panamá. Las poblaciones de la vertiente del Pacífico de Costa Rica y de Panamá se pueden diagnosticar de todas las demás poblaciones y aquí se describen como una nueva especie. El taxón *B. melanochlorus* está restringido a las poblaciones de las áreas faunisticas de Costa Rica como el Atlántico, Vertientes Montañosos y la Cordillera Central.**

Populations of toads referred to *Bufo melanochlorus* Cope, 1877 are found in wet forests on both Atlantic and Pacific versants of Costa Rica (Savage, 2002). Although there are ample series of specimens from the Southwest faunal area (sensu Savage, 2002:fig 15), populations in Atlantic, Montane Slopes and Cordillera Central, and Pacific Northwest faunal areas are documented by relatively small series of specimens that consist mostly of juveniles and subadults. As part of continued efforts to revise the taxonomy of Mesoamerican species of *Bufo*—so as to better reflect actual biodiversity in this region—we have examined series of specimens from throughout the geographic range of *B. melanochlorus*.

MATERIALS AND METHODS

General terminology and format for diagnoses and description follow that of Mendelson (1997). Foot-webbing formulae follow the system summarized by Savage (2002). Museum abbreviations are those proposed by Leviton et al. (1985), with the following addition: UCR for the Museo de Zoología, Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria Rodrigo Facio, San José, Costa Rica. We follow Tyler et al. (2001) in our usage of the term "parotoid gland."

We examined specimens for fixed morphological and color pattern differences. Species recognition follows the Phylogenetic Species Concept (Cracraft, 1983). Because we adhere to this concept, we considered groups, which are geographically isolated and diagnosable, different species.

The following morphological measurements were taken from adult specimens: snout–vent length (SVL), head length (HL), head width (HW), tibia length (TIB), tarsus length (TAR) foot length (FL), width of tympanum (TYM), length of parotoid gland (PARL), maximum width of parotoid gland (PARW), length of supratympanic crest (SPTYM), and length of postorbital crest (PORB). These variables, which represent repeatable morphological landmarks, were measured with digital calipers, rounded to nearest 0.1 mm. Sex of individuals was determined by presence/absence of male secondary sexual characters (nuptial excresences and/or vocal slits), or by direct examination of gonads.

We compared means between sexes and among species of 66 adult males and 39 adult females using ANCOVA, for all variables with SVL as the covariate. We compared mean SVL using a *t*-test. Statistical analyses were performed using SAS (SAS Institute, vers. 8). Because of limited availability of museum specimens of adult *B. melanochlorus*, our samples for this study are heavily skewed (especially for males). Nevertheless, we used morphometric analyses to assess variation in body shape. These analyses should be taken as preliminary; more thorough sampling will be required before robust conclusions may be drawn.

SPECIES ACCOUNTS

Bufo aucoinae sp. nov.
Figures 1–3

Bufo melanochloris.—Savage and Villa, 1986 [In part].

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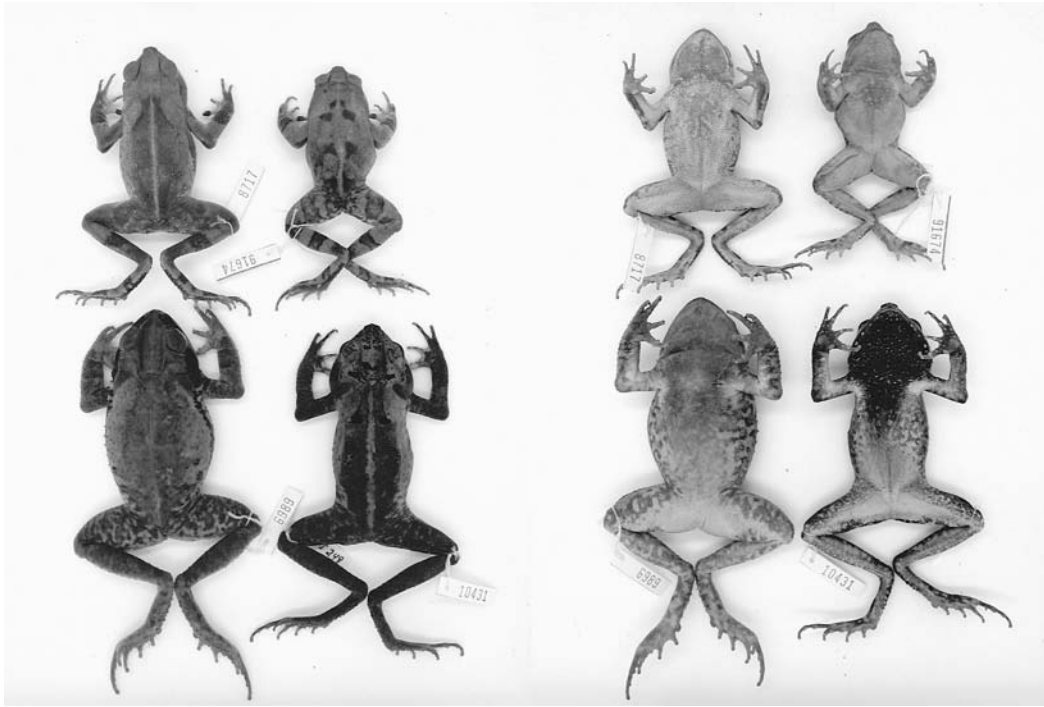

FIG. 1. Dorsal (left) and ventral (right) pattern variation among adult male *Bufo aucoinae* and *Bufo melanochlorus*. *Bufo aucoinae*: top left, UCR 8717 (holotype, SVL = 61.4 mm); top right, KU 91674 (SVL = 50.3 mm). *Bufo melanochlorus*: bottom left, UCR 10431 (SVL = 72.3 mm); bottom right, UCR 6989 (SVL = 73.6 mm).

Bufo melanochlorus.—Savage, 2002 [In part]; Frost, 2002 [In part].

Holotype.—UCR 8717, an adult male from the airport at the town of Aguabuena, Distrito Sierpe, Osa Peninsula, Puntarenas Province, Costa Rica (approximately 8°26′N, 83°38′W).

Paratypes.—All from Puntarenas Province, Costa Rica. Males: UCR 2082, from Eucalipto, Rincón de Osa, Sierpe, Osa; UCR 12240 and 12996 from bridge over Quebrada Cañaza, Golfito, Golfito; KU 91663 and 91665 from Río La Viejo, 30 km east of Palmar Norte, 100 m; KU 91668 from 2 km northwest of Dominical, 10 M; LCAM-CRE 6538 from 7 km south-southwest of Rincón Carretera al Pacifico; LACM-CRE 7083 from Rio La Vieja, 18.7 mi [30.1 km] by road east of Palmar Norte, 110 m; 8031 from 4.2 km northwest by road from Villa Neily, 20 m. Females: UCR 0894 from Boscosa, Aguabuena, Sierpe, Osa; UCR12433 from Parque Nacional Esquinas, Sendero La Trocha, Golfito; UCR 12239 and 12997 from bridge over Quebrada Cañaza, Golfito; UCR 14092 from La Gamba, Golfito, Golfito; KU 116978 from 8 km east-northeast of Palmar Norte, 90M; KU 65535 from Quebrada Boruca, 22 km east of Palmar Norte, 45M; KU 65536–65538 from 12.3 km west-northwest of Villa Neily, 25 m; LACM-CRE 6550 from Rincón Airport, 3 km west of Rincón, 25 m; LACM-CRE 9357 from 6 km southwest of Rincón de Osa; Savage Woods, 10 m; LACM-CRE 9647 from 7.5 km southwest of Rincón de Osa, Quebrado Rayo, 20 m.

Referred Specimens.—See Appendix 1.

Diagnosis.—A large species of *Bufo* (males to 67.2 mm SVL; females to 104.5 mm SVL) having the following combination of characters: (1) tympanum small, 12.3–18.4% head length in males, 11.2–15.5% in females; (2) preorbital and pretympanic crests poorly developed, or absent, in both sexes; (3) tibia short 42–50% of SVL; (4) feet relatively short 40–47% of SVL; (5) dorsal skin evenly covered with tiny spiculae, spiculae in males smaller and more concentrated than in females; (6) lateral row of tubercles present as a series of low, rounded tubercles in males, in females as a series of large sharply pointed spiculae; (7) vocal slits present, bilateral, small; (8) *m. interhyoideus* forming a small, unilobed unpigmented vocal sac; (9) snout sharply pointed in dorsal view, rounded in profile; (10) cranial crests low, thin; (11) parotoid glands small, distinctly triangular; (12) tips of digits same color as rest of digit.

Bufo aucoinae (Figs. 1–3) is similar to *B. melanochlorus* (sensu stricto) but differs by lacking

transverse folds between parietal crests, lacking or having poorly developed pretympanic and preorbital crests, having a relatively unmarked venter, and by having the *m. interhyoideus* forming a small, unpigmented vocal sac. *Bufo melanochlorus* has transverse folds between the parietal crests (Fig. 2), cranial crests that are greatly elevated vertically, distinct pretympanic and preorbital crests, a black throat and chest with mottling on the flanks, and *m. interhyoideus* forms a larger, heavily pigmented vocal sac. Morphometrically, males of *B. aucoinae* differ from *B. melanochlorus* by having relatively smaller HL, HW, TYM, and PARW; females of *B. aucoinae* have a larger TYM and PORB. Males of *B. aucoinae* are smaller (SVL) than are males of *B. melanochlorus*. Morphometric statistics are presented in Table 1.

FIG. 2. Skin texture of the dorsal surface of the area between the cranial crests of *Bufo aucoinae* (left, holotype, UCR 8717) and *Bufo melanochlorus* (right, UCR 8506) showing the distinctive folds in *B. melanochlorus*.

Description of Holotype.—Body robust; head wider than long, width 34.5% SVL, length 32.6% SVL; snout sharply pointed in dorsal view, rounded in profile, rostral keel absent; canthal, supraorbital, supratympanic, postorbital, and parietal crests present, low, thin; preorbital and pretympanic crests reduced, barely distinct; skin on top of head coosified with underlying cranial bones; nostril protuberant, directed dorsolaterally; canthus rostralis forming raised, canthal crest; loreal region slightly concave; lip distinct, rounded; suborbital crest present, barely distinct, extending from angle of the jaw anteriorly to nearly to level of nostril; notch at symphysis of upper jaw present; eye–nostril distance 62.3% diameter of orbit; tympanum distinct, nearly round; tympanic annulus distinct. Forelimb short, robust; hand broad, with short, slender fingers; relative length of fingers II < IV < I < III, webbing and lateral fringe on fingers absent; tips of fingers not enlarged, smooth dorsally, demarcated proximally by distinct dermal fold; palmar tubercle distinct, large, subcircular; pollical tubercle smaller than palmar tubercle, ovoid; subarticular tubercles distinct, elevated, triangular in profile, single except distal tubercle on Fingers I, III, IV bifid; supernumerary tubercles of unequal size, small, distinct, scattered evenly over palm and ventral surfaces of fingers; nuptial excrescences present as brown granular patches on dorsal surfaces of Finger I and medial surface of Finger II. Hind limbs long, slender, tibia length 47.2% SVL; foot length 43.8% SVL; tarsal fold absent; outer metatarsal tubercle very small, elevated, ovoid; inner metatarsal tubercle slightly larger than outer metatarsal tubercle, distinctly elevated, ovoid; toes long, slender, relative lengths of toes I < II < V < III < IV; lateral fringe present on all toes; webbing thin, webbing formula **I**2—2**II**1—3**III**2—31/2 **IV**31/2—2**V**; tips of toes not enlarged, smooth dorsally, demarcated proximally by distinct dermal fold; subarticular tubercles distinct, elevated, triangular in profile, single; supernumerary tubercles unequal in size, distinct, distributed evenly over ventral surfaces of foot and toes.

Skin on dorsum of body with evenly distributed small, spiculate tubercles of relatively equal size, becoming larger and less numerous laterally, enlarged tubercles in two paravertebral rows, parotoid smaller than eyelids, triangular, extending posteriorly at about 45° to midline of body; lateral row of enlarged tubercles present or weakly spiculate; dorsal surface of head with many, small, spiculate tubercles scattered in interspaces between cranial crests; folds in skin between parietal crests absent; dorsal surfaces of limbs covered with small spiculate tubercles; skin on throat and other ventral surfaces granular.

Choanae small, ovoid, widely spaced, the distance between them (5.5 mm) about 4.5 times the width of one (1.2 mm); teeth and odontoids absent; tongue long, ovoid, about four times as long as wide, free posteriorly for about one-fourth its length; vocal slit bilateral, small, about one-fourth length of tongue.

Color of Holotype.—In preservative (ethanol), dorsum of body dull brown medially, becoming gray-brown laterally; top of head gray-brown; dorsal tubercles with red-brown apices; crests with red-brown surfaces, color reduced on preorbital crest; lateral row of tubercles coincides with boundary between dorsolateral coloration and dark brown lateral coloration; flanks slightly paler than dorsolateral area; dorsal markings consist of a thin, pale-gray dorsal stripe; dorsal surfaces of arms and legs dull brown, many of the tubercles thereupon with red-brown apices; forearm with distinct, wide transverse bar darker than adjacent areas; dark brown lateral coloration extending anteriorly over tympanic area; loreal and suborbital regions dull brown; lip pale

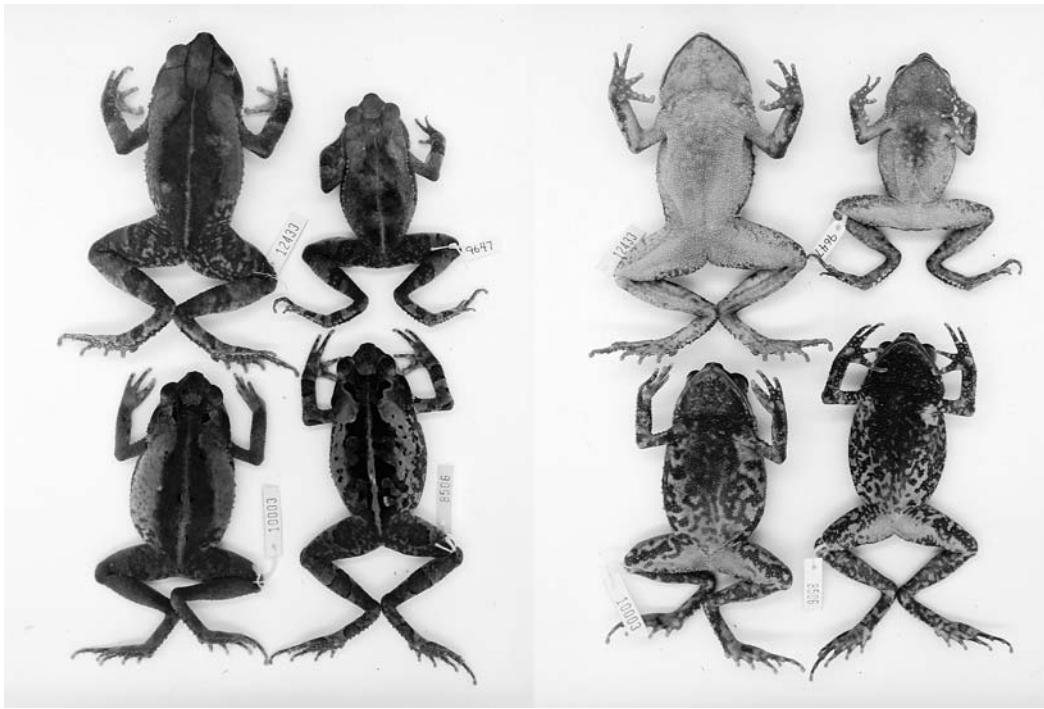

FIG. 3. Dorsal (left) and ventral (right) pattern variation among adult female *Bufo aucoinae* and *Bufo malanochlorus*. *Bufo aucoinae*: top left, UCR 12433 (SVL = 75.7 mm); top right, LACM-CRE 9647 (SVL = 60.2 mm). *Bufo melanochlorus*: bottom left, UCR 10003 (SVL = 69.5 mm); bottom right, UCR 8506 (SVL = 68.5 mm).

cream; parotoid glands gray-brown; dorsal surfaces of Fingers III and IV dull brown with distinct transverse cream line separating tips; Fingers I and II cream throughout; dorsal surfaces of Toes I, II, III dull cream; Toes IV and V gray-brown dorsally with cream tips; throat dull cream, becoming paler cream anteriorly; venter pale cream; ventral surfaces of hands dull cream with most tubercles pale cream; ventral surfaces of forearms dark brown; ventral surfaces of humeral areas dull cream; ventral surfaces of legs dull cream.

Measurements of Holotype (in mm).—SVL 61.4, tibia length 29.0, foot length 26.9, head length 20.2, head width 21.2, orbit diameter 7.7, tympanum diameter 2.9, supratympanic crest length 4.8, parotoid gland length 8.6, parotoid gland width 3.9.

Color in Life.—A photograph of an amplectant pair of *B. aucoinae* was presented by Savage (2002:pl. 80).

Variation.—Morphometric variation among specimens examined is summarized in Table 1. Males (Fig. 1): most specimens have a color pattern similar to that of the holotype. Middorsal stripe may be faint (e.g., KU 6538) or distinct (e.g., UCR 8717). Some males (e.g., KU 91674) have spots similar to *B. melanochlorus*, but these are usually gray rather than black. Ventral surfaces are usually plain, lacking dark markings on throat and venter; faint mottling is present in a few specimens (e.g., KU 91678), usually concentrated on chest and throat. Some males (e.g., UCR 91672) resemble the holotype by having the dorsal spiculae and cranial crests heavily keratinized such that they appear distinctly red-brown in color, contrasting sharply with surrounding skin. Females (Fig. 3): individuals vary in dorsal color and pattern. Some specimens (e.g., LACM-CRE 9318) have a dorsal pattern consisting of dull brown ground color with scattered dark brown, irregular, paired spots, but most lack dorsal spots, and are darker middorsally than in dorsolateral areas. Some females (e.g., UCR 12239) resemble the male holotype by having the dorsal spiculae and cranial crests heavily keratinized such that they appear distinctly red-brown in color, contrasting sharply with the surrounding skin. Ventral surfaces are usually plain, lacking dark markings on the throat and venter; faint mottling is present in a few specimens (e.g., LACM-CRE 9318), usually concentrated on the chest and throat. At least one female (UCR 14232) has a dorsal pattern almost identical to *B. melanochlorus*, but can be distinguished by lacking folds between

TABLE 1. Morphometric variation in *Bufo aucoinae* and *Bufo melanochlorus*. Mean ± 1 SD above range (in parentheses); all measurements in millimeters.

Variable	*Bufo aucoinae*		*Bufo melanochlorus*	
	Males N =62	Females N = 30	Males N = 4	Females N = 9
Snout–vent length†	52.5 ± 5.2 (42.0–67.2)	70.7 ± 12.1 (50.5–95.0)	68.6 ± 9.0 (55.1–73.6)	73.6 ± 18.4 (50.4–106.7)
Tibia length	25.0 ± 2.5 (19.8–32.3)	32.4 ± 5.3 (23.1–41.9)	32.4 ± 3.4 (27.3–34.9)	33.9 ± 8.0 (24.5–48.0)
Tarsus length[1]*	15.0 ± 1.5 (11.9–19.2)	19.6 ± 3.0 (14.5–24.7)	19.2 ± 1.7 (16.7–20.3)	20.5 ± 4.7 (14.8–29.1)
Foot length	22.5 ± 2.4 (17.7–29.2)	28.5 ± 4.6 (20.8–36.7)	29.0 ± 3.8 (23.5–30.2)	29.8 ± 7.3 (17.8–43.4)
Head length[1]***	18.3 ± 1.7 (14.9–23.2)	24.7 ± 3.8 (17.9–31.1)	24.9 ± 3.5 (19.7–27.1)	25.5 ± 5.9 (18.2–36.2)
Head width[1]**	19.2 ± 1.9 (15.9–25.3)	26.3 ± 4.8 (18.4–35.7)	26.3 ± 3.6 (20.8–28.3)	27.8 ± 6.8 (19.7–40.6)
Tympanum diameter[1]***,[2]	2.7 ± 0.4 (1.9–3.7)	3.3 ± .06 (2.0–4.0)	2.9 ± 0.6 (2.2–3.4)	2.9 ± 0.7 (2.1–4.4)
Supratympanic crest	3.8 ± 0.5 (2.8–5.3)	5.4 ± 1.1 (3.6–7.6)	4.9 ± 0.9 (3.6–5.7)	5.7 ± 1.7 (3.7–8.8)
Postorbital crest[2]	5.8 ± 0.6 (4.6–7.6)	7.5 ± 1.2 (4.7–10.0)	7.2 ± 1.1 (5.6–8.0)	7.0 ± 1.5 (4.9–9.6)
Parotoid length	8.3 ± 1.1 (5.6–11.1)	10.3 ± 2.6 (5.3–15.7)	9.2 ± 2.2 (7.6–12.3)	9.9 ± 3.2 (6.5–16.1)
Parotoid width[1]***	3.6 ± 0.5 (2.7–4.6)	4.9 ± 1.2 (2.9–7.3)	5.0 ± 0.4 (4.8–5.5)	5.0 ± 1.6 (2.8–8.5)

† t-test (males; df = 65) $P = 0.04$; (females; df = 38) $P = 0.65$.
[1] ANCOVA (males; df = 62); ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$.
[2] ANCOVA (females; df = 35); $P < 0.0001$.

postorbital crests (Fig. 2) and by lacking distinct dark markings on throat and venter. Juveniles show similar variation in color pattern to adults, but the ventral region is darker. This dark ventral coloration fades to the typical plain cream color as individuals mature.

Etymology.—This species is named in honor of Lisa Louise Aucoin who passed away August 2001 shortly after returning from Costa Rica. Lisa's passion for herpetology and biogeography of Central America was impressive. Unfortunately her life was cut short while she was a graduate student at Southeastern Louisiana University working with Brian Crother and Mary White.

Distribution and Ecology.—The range of *B. aucoinae* coincides approximately with the Southwest faunal area of Costa Rica, as defined by Savage (2002:fig 15.7), and a single specimen is known from the adjacent region in Chiriqui, Panama (Fig. 4). This is the first report of this species in Panama (Ibáñez et al., 2001), although its occurrence there was predicted by Savage (2002, as *B. melanochlorus*); the Panamanian specimen (KU 96331) was collected by C. W. Myers in 1965. This species occurs in wet tropical forest habitat and breeds in streams during the dry season (Savage, 2002; J. Malone, pers. comm; M. Ryan, pers. comm).

Tadpoles.—The tadpole of *B. aucoinae* has not been described.

Bufo melanochlorus Cope, 1877
Figures 1–3

Bufo valliceps.—Cope, 1875; Leenders, 2001: pl. 9.

Bufo melanochlorus.—Cope, 1877, Proc. Amer. Philos. Soc. 17: 85–98. Holotype: USNM 30592. Type-locality: East or eastern Cantón de Limón, Provincia de Limón, Costa Rica. Type locality restricted by Savage, 1974, Rev. Biol. Trop. 22:71–122. Savage, 2002 [In part]; Frost, 2002 [In part].

Bufo melanochloris.—Taylor, 1952 [Incorrect subsequent spelling]; Cochran 1961; Greding, 1972; Savage, 1974; Frost, 1985; Savage and Villa, 1986 [In part].

Diagnosis.—A large species of *Bufo* (males to 73.6 mm SVL; females to 106.7) having the following combination of characters: (1) tympanum small 10.3–12.9% head length in males, 9.3–13.1% in females; (2) preorbital and pretympanic crests well developed in both sexes; (3) tibia short 45–50% SVL; (4) feet relatively short 35–44% SVL; (5) dorsal skin unevenly covered with small, low, rounded spiculae, distinct transverse folds between parietal crests; (6) lateral row of tubercles present as a series of medium-sized sharply pointed spiculae; (7) vocal slits present,

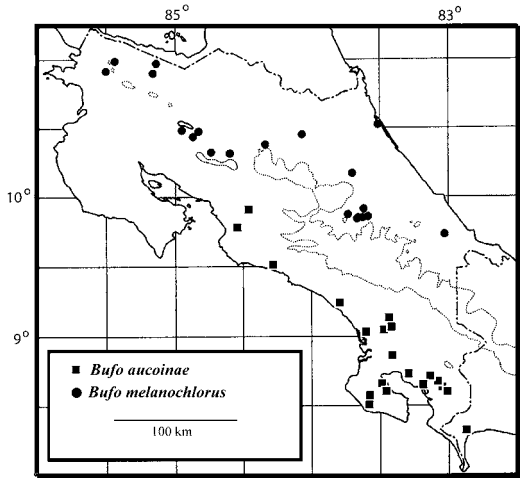

FIG. 4. Map of Costa Rica, showing distributions of *Bufo aucoinae* and *Bufo melanochlorus*. Dotted lines represent the 1500 m contour. Map was modified directly from Savage (2002:map 7.13).

bilateral, small; (8) *m. interhyoideus* forming a large, unilobed heavily pigmented vocal sac (9) snout sharply pointed in dorsal view, rounded in profile; (10) cranial crests high, thin; (11) parotoid glands small, elongate; (12) tips of digits same color as rest of digit, or distinctly paler.

Bufo melanochlorus (Figs. 1–3) is similar to *B. aucoinae* but differs by having transverse folds between parietal crests, cranial crests that are greatly elevated vertically, distinct pretympanic and preorbital crests, a black throat and chest with mottling on flanks, and *m. interhyoideus* forming a larger, heavily pigmented vocal sac. *Bufo aucoinae* (Figs. 1–3) lacks transverse folds between parietal crests, lacks or has poorly developed pretympanic and preorbital crests, has a relatively unmarked venter, and the *m. interhyoideus* forms a small, unpigmented vocal sac. Morphometrically, males of *B. melanochlorus* differ from *B. aucoinae* by having relatively larger HL, HW, TAR, TYM, and PARW; females of *B. melanochlorus* have a smaller TYM and PORB. Males of *B. melanochlorus* are larger (SVL) than are males of *B. aucoinae*. Morphometric statistics are presented in Table 1.

Color in Life.—Savage (2002:pl. 81) includes a photograph of a subadult *B. melanochlorus*. Leenders (2001:pl. 9) presented a color photograph (as *B. valliceps*) of what appears to be a subadult specimen. A black-and-white illustration of this species, showing general color pattern was presented by Taylor (1952:fig. 5; KU 30275).

Variation.—Morphometric variation among specimens examined is summarized in Table 1. Males (Fig. 1): dorsum is generally gray, two specimens (KU 32819, UCR 10431) have 2–3 pairs of irregular black dorsal spots. All specimens have a middorsal stripe, which is thin in two specimens (KU 32819, UCR 6989) and thick in the remaining two specimens (UCR 10430–31). Dorsolateral surfaces are generally paler gray than the middorsum. The throat is generally black, and this color extends onto the ventral surfaces of the body, becoming mottled posteriorly. Females (Fig. 3): dorsum is generally gray with 3–5 pairs of irregular black spots, and a middoral stripe that may be thin (e.g., UCR 12689) or thick (e.g., UCR 7649). The dorsal pattern in females is quite variable; some females (e.g., UCR 8217, 12656, 12689, 10003) almost completely lack the paired black spots. The throat is generally black, and this color extends onto the ventral surfaces of the body, becoming mottled posteriorly. Juveniles show similar variation in color pattern to the adults; the dark ventral coloration of the juvenile persists in the adults.

Distribution and Ecology.—The range of *B. melanochlorus* includes the Atlantic, Montane Slopes and Cordillera Central, and the extreme southern portion of the Pacific Northwest faunal areas of Costa Rica, as defined by Savage (2002:fig. 15.7). This species occurs in wet tropical forests, and breeds in streams during the dry season.

Tadpoles.—The tadpole of *B. melanochlorus* has not been described.

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APPENDIX 1

Specimens Examined

Note: Apparent inconsistencies in the geographic data represented here reflect individual variations in the original locality descriptions that accompany the specimens; we thought it unwise to edit the original, raw locality data.

Bufo aucoinae: COSTA RICA: PUNTARENAS: Peninsula de Osa, near Rincón, Camp Seattle (UMMZ 123619–20); Peninsula de Osa, Rincón Agua Buena (UMMZ 125860); Peninsula de Osa, 4.5 mi south of Rincón (UMMZ 125861); Peninsula de Osa (UMMZ 129018–20); Osa Peninsula, Corcovado National Park, near Río Pavo on Los Patos–Sirena trail (UMMZ 190355); Rincón de Osa, 30 m (LACM-CRE 10208); Quebrada Aguabuena, Rincón de Osa (LACM 114266); Tropical Science Center Field Station, Finca de Osa (LACM 114347–38); 6 km southwest of Rincón de Osa, Savage Woods, 10 m (LACM-CRE 9305, 9318, 9357–60); 7 km southwest of Rincón de Osa, Savage Woods, 10 m (LACM-CRE 9550); 3 km southwest of Rincón de Osa, 0.5–1.0 km south of Osa Station, 40 m (LACM-CRE 7237, 8316, 9200, 9322, 9344); 8 km southwest of Rincón de Osa (LACM-CRE 9546–47); 14 km east-southeast of Palmar Norte, Quebrada Coobó, 80–100 m (LACM-CRE 8764–65); 7.5 km southwest of Rincón de Osa, Quebrada Rayo, 20 m (LACM-CRE 9647); Corcovado National Park, Sirena Station (LACM-CRE 8974, 8976); 4.2 km northwest by rd from Villa Neily, 20 m (LACM-CRE 8031); 18.7 rd mi east of Palmar Norte, Río La Vieja, 110 m (LACM-CRE 7083); Río Ferruviosa, 7.2 km south of Rincón de Osa, 20 m (LACM-CRE 7235); Pan-Am Hwy at Río Nuevo, 3.2 km northwest of Villa Neily (LACM-CRE 7109); Pan-Am Hwy, 14.5 km northwest of Villa Neily at Río Claro, 20 m (LACM-CRE 7110); Pan-Am Hwy, 4.8 km southwest of Buenos Aires at Río Ceibo, 320 m (LACM-CRE 7112); 3.2–4.8 km west of Palmar Norte, on rd to Puerto Cortés, 10 m (LACM-CRE 7101); Rincón (LACM-CRE 705); Rincón de Osa (KU 145462); 5 km southwest of Rincón de Osa, Savage Woods, 10 m (LACM-CRE 3498, 3500); 3 km west-southwest of Rincón de Osa, near airfield, 60 m (LACM-CRE 3508); 7 km south-southwest of Rincón, Carretera al Pacifico, 20 m (LACM-CRE 6537); Rincón airport, 25 m (LACM-CRE 6550); Quebrada Aguabuena, 2.5 km southwest of Rincón, 25 m (LACM-CRE 6566); 3 km west of Rincón, near airport, 25 m (LACM-CRE 3109); 5.5 km south-southwest of Rincón, 20 m (LACM-CRE 3196); 3 km west-southwest of Rincón de Osa, 40 m (LACM-CRE 6623); Quebrada Boruca, 22 km east of Palmar Norte, 45 m (KU 65535); 12.3 km west-northwest of Villa Neily, 25 m (KU 65536–38); Río La Viejo, 30 km east of Palmar Norte, 100 m (KU 91663–65); 2 km northwest of Dominical, 10 m (KU 91666, 91668); Río Zapote, 8 km east of Palmar Norte, 70 m (KU 93900–01); Palmar Norte, Quebrada Grande (UCR 7875); 4.5 km west of Rincón de Osa, 45 m (KU 102139–42, 102147–49); 8 km east-northeast of Palmar Norte, 90 m (KU 116978–79); Osa, Lindavista (UCR 14232); Golfito, Quebrada Cañaza (UCR 14322–24); Golfito, Quebrada La Gamba (UCR 14325); Golfito, Puerto Jiménez, Sirena (UCR 11279, 11284–85, 11840, 12118); Golfito, Naranjal (UCR 11966, 12039–40); Golfito, Quebrada Cañaza pte. (UCR 12239–40, 12996–97); Golfito, Quebrada La Gamba (UCR 12998, 14002, 14092); Golfito, Parque Nacional Esquinas, sendero La Trocha (UCR 12433); Aguabuena, BOSCOSA (UCR 893–94); 1 km southeast of Aguabuena (UCR 1098); Rincón de Osa, Eucalipto (UCR 2082–84, 4553–57, 4593); Rincón de Osa, aeropuerto (UCR 4574, 8717). SAN JOSÉ: Parque Nacional Braulio Carrillo, Vázquez de Coronado, Dulce Nombre Jesús (UCR 8217, 9454); 20 km southwest of San Isidro del General, 525 m (KU 65531–34, 65539–42, 91669, 91670–79); Montañas Jamaica, 1.4 rd mi north of Bijagual and 0.3 mi north-northeast [*sic*] of (TCWC 83998); Montañas Jamaica, 1.4 rd mi north of Bijagual and 0.6 rd mi north-northeast of Quebrada Tarcolitos (TCWC 84003); Parque Nacional Carara, 1.9 rd mi south of Río Tarcoles on Hwy 34, Quebrada Patos (TCWC 84055, 84127); Parque Nacional Carara, Montañas Jamaica, Quebrada Maquina/Tarcolitos (TCWC 84125);

near Parque Nacional Carara, Bajo Carara, Quebrada Surtubal (TCWC 84622). PANAMA: CHIRIQUI: 7.5 km north of Puerto Armuelles, 10 m (KU 96331).

Bufo melanochlorus: COSTA RICA: ALAJUELA: La Balsa (KU 139995); San Ramón, Peñas Blancas (UCR 8506); San Ramón, Angeles (UCR 10003); San Ramón, Angeles, Colonia Palmarena (UCR 11922, 12294); Upala, Dos Ríos, Bosque Pizote (UCR 10194); Upala, Dos Ríos, Brasilia (UCR 10430–31); San Carlos, centro Pocosol (UCR 7649); San Carlos, Florencia, Penjamo (UCR 13101); 0.5 km southwest of La Marina, on Río San Rafael, 480 m (LACM-CRE 515). CARTAGO: Turriabla, IICA, 1 mi south of main building, along east bank Río Reventazón, 600 m (LACM-CRE 690); Turriabla, Pavones, Buenavista Pte Río Chitaría (UCR 1684); Río Chitaría, 6.2 mi northeast of bridge over Río Reventazón on Turriabla–Peralta Rd, 775 m (LACM-CRE 7196); Turriabla, IAIA (KU 28356); Turriabla, IAIA, Río Reventazón (KU 32819); jct Río Tuis × Río Reventazón (KU 65530); Esquinas Bridge at Turriabla (KU 32809); Pavones, Turriabla (KU 139994, 139999–40000; UCR 6989–91); Turriabla, Tayutic, Moravia, Trocha Abierta (UCR 6022–24). GUANACASTE: Pitilla Biological Station, 600–1072 m (LACM-CRE 10423); Arenal, 520 m (LACM-CRE 6256); Tenorio, Las Flores (KU 32817–18); Liberia, Mayorga (UCR 5245). LIMÓN: Río Pacuare, around Pacuare (KU 30275–78); 10 km north-northwest of Los Diamantes (UMMZ 125468); Pococí, centro Guápiles (UCR 3227); Valle de Estrella (UCR 9530); centro Siquirres (UCR 12656); Siquirres, Alto Guayacán (UCR 12689).

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Auditory Sampling of Frogs: Detection Efficiency in Relation to Survey Duration

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ABSTRACT.—**Call surveys are used widely to assess distribution and abundance of anurans. The durations of these surveys often are based on convenience rather than on empirical analysis. Knowing how frog detection varies with survey duration is valuable for designing sampling schemes, yet few studies have examined the relationship between survey duration and detection efficiency. We conducted call surveys for frogs in central Texas to assess effects of survey duration on detection efficiency. We controlled analytically for temporal and environmental covariates that had the potential to confound our assessment of survey duration. Cumulative detection efficiency of all species was 94% for 15-min surveys and did not increase appreciably with longer durations up to 30 min. Detection efficiency for number of species was significantly higher for 15-min surveys than it was for 5-min surveys, and the variability of detection efficiency decreased with increasing survey duration. Detection efficiency for number of calling individuals of *Acris crepitans* and *Rana sphenocephala* did not differ among 5-, 10-, and 15-min surveys. Of the temporal and environmental covariates examined, only the year in which a survey was conducted was significantly associated with detection efficiency for number of species. None of the covariates was significantly related to detection efficiency for *A. crepitans* or *R. sphenocephala*. When sampling resources such as time and personnel are limited, knowledge about detection efficiencies is essential for allocating survey effort.**

Concerns about amphibian declines (Wake, 1991) have stimulated interest in developing better methods to monitor amphibian populations (Heyer et al., 1994). Call surveys have been proposed as a cost-effective method for assessing anuran distribution patterns and population trends. This method is based on the species-specific advertisement calls made by males of many frogs and toads during the breeding season. Such calls can be easily detected and quantified and provide evidence of species presence and a rough index of adult population size. Frog call surveys, often conducted by trained volunteers, are gaining widespread acceptance and application.

Despite the growing use of frog call surveys, few studies have assessed the accuracy of this method. One important methodological issue that has received little attention is detection efficiency in relation to duration of the call survey. Different amphibian monitoring programs use surveys of differing duration. For example, the North American Amphibian Monitoring Program (http://www.pwrc.usgs.gov/NAAMP/protocol/) and the long-running Wisconsin Frog and Toad Survey (Mossman et al., 1998) specify a listening time of 5 min at each site, but volunteers participating in Iowa's frog and toad survey are required to listen for 10 min at each site (Hemesath, 1998), and those in Texas (http://www.tpwd.state.tx.us/nature/education/tracker/amphibians/) and Ontario (Shirose et al., 1997) are instructed to listen for only 3 min.

Shirose et al. (1997) conducted frog call surveys of long duration and concluded that 3-min surveys were adequate to sample the presence/absence and calling intensity of most species in Ontario. Crouch and Paton (2002) determined detection probabilities for amphibian call surveys in Rhode Island and suggested that call surveys be conducted for 10 min to have a high probability (>90%) of detecting all species. However, listening times for most surveys appear not to be based on empirical evidence about the efficiency of survey duration; thus, the accuracy with which such surveys actually detect species that are present and calling is unclear.

Knowing the accuracy of detection is often useful for designing amphibian surveys. For example, sampling resources such as time and personnel are frequently limited, and decisions must be made about the duration and number of surveys that can be conducted with available resources. Increasing the duration of each individual survey usually means that a smaller number of surveys can be conducted, so knowl-

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edge about the gain in accuracy with increasing survey duration is critical.

In this study, we conducted frog call surveys in central Texas using a long (30-min) listening time to determine the presence of amphibian species. We then analyzed the results of those surveys to assess the effects of survey duration and other factors on detection efficiency. Other studies (Hemesath, 1998; Mossman et al., 1998; Shirose et al., 1997; Crouch and Paton, 2002) have generally used surveys of 2–10 min, and our preliminary analysis indicated that survey accuracy did not increase appreciably after 15 min; hence, we focused our analyses on 5-, 10-, and 15-min surveys.

Materials and Methods

Data Collection.—A total of 162 auditory surveys of breeding frogs were conducted at weekly intervals during spring and early summer of 1994–1997 at 14 known amphibian breeding sites within approximately 80 km of Waco, Texas. The sites included reservoirs, rivers, small ponds, and ephemeral wetlands. All locations were visited between 1900 and 2400 h. At each site, we conducted a 30-minute auditory survey, which was divided into six 5-min sampling intervals.

For each survey, we recorded survey date (in days since 1 January), survey location, survey year, time at the start of the survey (in min since midnight), air temperature at the start of the survey (°C), water temperature at the end of the survey (°C), wind force (Beaufort scale) at the start of the survey, approximate cloud cover at the start of the survey (%), and presence or absence of precipitation. Some upper categories of wind force had few observations, so we lumped data for original levels of wind force into three levels before analysis: 0 = Beaufort scale 0, 1 = Beaufort scale 1–3, and 2 = Beaufort scale 4–6. No Beaufort scale values above 6 were recorded during the surveys. Precipitation occurred during only four of the surveys used for data analysis, so this variable was not included in the analysis.

For each 5-min sampling interval within the 30-min survey, we recorded the number of individual frogs calling by species, using the following numerical categories: 0, 1, 2, 3–5, 6–10, and more than 10. When a range was observed for the number of individuals calling (e.g., 3–5 frogs), the midpoint of the range was used for statistical analysis. We estimated that the maximum number of calling frogs of any one species in the populations we studied was approximately 30; thus, when more than 10 frogs were recorded as calling, we used the midpoint between 11 and 30 (20.5) for statistical analysis. Use of such numerical categories or call intensity indices is common in analyses of frog call surveys because of the difficulty of estimating numbers of frogs calling, especially in large choruses (Shirose et al., 1997; Hemesath, 1998; Mossman et al., 1998).

In 59 of the original 162 surveys, no frogs called during the 30-min sampling interval. Surveys in which no frogs called were not included in the present analysis because we wanted our assessment of survey duration efficiency to be based on surveys in which frogs were known to be present and calling. This approach prevented our assessment of efficiency from being confounded with the presence or absence of a frog. Surveys from sites with a single survey and surveys with missing weather data also were eliminated, leaving a total of 90 surveys from 12 sites on which analyses were implemented.

All surveys were conducted by one of the authors or by field assistants, who were biology students that received extensive training prior to surveys. One of the authors participated in about 75% of the surveys. Species detected during surveys and included in the analysis were *Acris crepitans*, *Bufo nebulifer*, *Hyla versicolor*, *Gastrophyrne olivacea*, *Pseudacris clarkii*, *Pseudacris streckeri*, *Rana catesbeiana*, *Rana sphenocephala*, and *Rana blairi*. *Bufo woodhousii* was heard at one site on one occasion; this observation was not included in the data analysis, and no results are reported for this species. We complied with all institutional regulations concerning the care and use of animals. Permits to study amphibians at Mother Neff State Park, Fort Fisher State Park, and Meridian State Park were granted by the Texas Parks and Wildlife Department.

Cumulative Detection Efficiency.—Cumulative detection efficiencies were calculated for number of species at 5-, 10-, 15-, 20-, 25- and 30-min intervals for the 30-min auditory survey. Cumulative detection efficiency is the cumulative number of species detected at the end of a particular duration (5, 10, 15, 20, 25, or 30 min), divided by the total number of species detected by the end of the entire 30-min survey. It represents the proportion of all the species present and calling at least once during the 30-min survey that were detected by the end of the chosen duration. Mean cumulative detection efficiency for number of species was calculated for each of the 12 survey sites, and mean values for sites were then averaged for each duration interval and plotted as a species accumulation curve (Shiu and Lee, 2003). The mean (as opposed to individual values of) cumulative detection efficiency for each site was used to calculate each duration interval value because efficiencies may have been correlated within sites; such dependencies can lead to underestimates of variation (Hurlbert, 1984). By lumping efficiencies within sites (i.e., using sites not

surveys as the unit of observation), we obtained estimates of precision (SEs) for cumulative detection efficiency that do not assume individual surveys at the same site were independent.

Influence of Survey Duration.—To assess effects of survey duration on detection efficiency, we derived three dependent variables for subsequent general linear model analyses: detection efficiency for number of frog species, detection efficiency for number of *A. crepitans*, and detection efficiency for number of *R. sphenocephala*. Other species were encountered too infrequently to permit separate quantitative analyses of their detection. Using 30-min surveys during which at least one frog called, we randomly selected surveys for analysis of their first 5-, 10-, or 15-min results. We computed detection efficiency for number of frog species as the number of species detected during the randomly selected survey duration (5, 10, or 15 min) divided by the number of species detected by the end of the 30-minute survey. Similarly, detection efficiency for a given species was calculated as the number of individuals detected during the randomly selected survey duration divided by the number of individuals of that species detected by the end of the 30-min period.

The relationship between detection efficiency and survey duration was the focus of our analysis, but we wanted to control analytically for several covariates that had the potential to influence the results. In addition to survey duration, we therefore included the following explanatory variables (covariates) in our modeling: survey date, survey location, survey year, time at the start of the survey, air temperature at the start of the survey, water temperature at the end of the survey, wind force at the start of the survey, and cloud cover at the start of the survey.

Using a general linear model (PROC GLM, SAS Institute, SAS/STAT user's guide, vers. 8. vol. 2, Cary, NC, 1999) to implement analysis of covariance (Huitema, 1980), we assessed whether each dependent variable was associated with the explanatory variables. Survey duration, location, and year, as well as wind force were analyzed as classification variables, and the remaining explanatory variables were analyzed as continuous variables. Before analyses, we applied an arcsine square-root transformation (Zar, 1999) to the proportions representing detection efficiency. Residual plots, histograms, and normal-probability plots confirmed that each model met statistical assumptions (Neter et al., 1989) regarding linearity and error-term normality and variance.

General linear models also assume that error terms are independent (Neter et al., 1989). Surveys conducted at the same locations but on different days or during different years had the potential to be correlated. Serial correlation problems can often be avoided by including appropriate explanatory variables in the model (Neter et al., 1989). Our inclusion of survey location, year, and date in each model reduced the potential for dependence among error terms. For each model, residual plots (Neter et al., 1989) confirmed that error terms were not correlated.

We assessed the effect of each explanatory variable based on Type III sums of squares, which reflect the influence of a variable after all other explanatory variables in the model have been accounted for (SAS Institute, SAS/STAT user's guide, vers. 8. vol. 2, Cary, NC, 1999). Using a Tukey-Kramer multiple comparison adjustment of *P*-values, we conducted pairwise comparisons of least-squares means of detection efficiency among survey durations; least-squares means are means that are corrected for other variables in the model (SAS Institute, SAS/STAT user's guide, vers. 8. vol. 2, Cary, NC, 1999). For all analyses, α was 0.05. The statistical significance of effects of survey duration and other explanatory variables is based on transformed detection efficiencies, but summary statistics reported for detection efficiencies and explanatory variables are for untransformed data.

Results

Cumulative Detection Efficiency.—The cumulative detection efficiency for number of species (percent of all species present that were detected) was 0.77 ± 0.04 (mean $\pm$ 1 SE) at the end of the first 5-minute interval (Fig. 1). This indicates that an average of 77% of species known to be present and calling at least once during a 30-min survey were detected in the first 5 min of the survey. Cumulative detection efficiency for species increased to 0.94 ± 0.02 at 15 min, and then increased minimally during the last 15 min of the survey (Fig. 1). New species were heard for the first time after 5 min in 32.3% of the surveys and after the first 15 min in 11.1% of the surveys.

Influence of Survey Duration.—The following sample sizes indicate how surveys were spread across the variable categories. For number of species, 3–15 surveys were conducted at each of 12 locations; 2–14 surveys were conducted at each of nine locations for *A. crepitans*, and 3–9 surveys were conducted at each of seven locations for *R. sphenocephala*. The number of surveys per year was 19 (1994), 47 (1995), 15 (1996), and 10 (1997) for number of species; 14 (1994), 22 (1995), seven (1996), and four (1997) for *A. crepitans*; and three (1994), 27 (1995), six (1996), and four (1997) for *R. sphenocephala*. The number of surveys for each wind-force category was 47 (0), 32 (1), and 11 (2) for number of species; 26 (0), 15 (1), and six (2) for *A. crepitans*; and 22 (0), 15 (1), and three (2) for *R. sphenocephala*. Summary

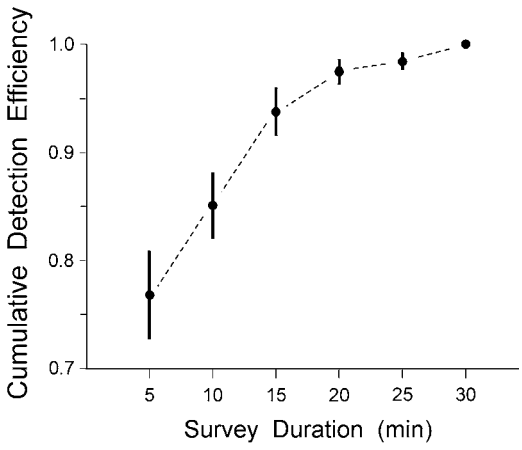

FIG. 1. Cumulative detection efficiency (proportion of frog species detected) for various intervals of a 30-min call survey. Means (dots) ± 1 SE (lines) are based on 90 surveys conducted at 12 locations in central Texas.

statistics for the other variables in our models (Table 1) characterize additional aspects of the temporal and physical conditions in which we studied effects of survey duration.

Survey duration significantly influenced detection efficiency for number of species ($F = 4.17$, $P = 0.020$) but not detection efficiency for number of *A. crepitans* ($F = 0.02$, $P = 0.978$) or number of *R. sphenocephala* ($F = 1.01$, $P = 0.381$). Except for survey year in the model for number of species, none of the other explanatory variables was significantly associated with detection efficiency (Table 2). Pairwise comparisons of least-squares means indicated that detection efficiency for number of species differed between 5- and 15-min surveys (Fig. 2). For *A. crepitans*, mean detection efficiency ± 1 SE (*N*, range) for number of individuals in the 5-, 10-, and 15-min surveys was 0.77 ± 0.10 (17, 0.0–1.0), 0.82 ± 0.10 (15, 0.0–1.0), and 0.93 ± 0.07 (15, 0.0–1.0), respectively. For *R. sphenocephala*, mean detection efficiency for number of individuals ± 1 SE (*N*, range) for the 5-, 10-, and 15-min surveys was 0.57 ± 0.13 (14, 0.0–1.0), 0.81 ± 0.08 (12, 0.25–1.0), and 0.79 ± 0.11 (14, 0.0–1.0), respectively.

DISCUSSION

Cumulative Detection Efficiency.—Protocols of many frog call surveys specify a 5-min listening time at each site, although some specify 10 min and others only 3 min. Using long duration surveys similar to ours, Shirose et al. (1997) found that most of the frog species at their sites in Ontario (*Bufo americanus*, *Hyla versicolor*, *Pseudacris crucifer*, *Rana clamitans*, and *Rana pipiens*) were detected in the first minute of a survey, although in 18.2% of the surveys a species was heard for the first time after the initial 5 min of the survey and, in a few cases, species were not detected until after 15 min. They also determined that increasing the survey duration from 3 to 5 min did not significantly increase the reliability of assessment of calling intensity (i.e., number of individuals) by different observers. Crouch and Paton (2002) found the average detection probability (i.e., efficiency) for species to be 81% in the first 2 min of their surveys of seven Rhode Island frogs (*Bufo americanus*, *Hyla versicolor*, *Pseudacris crucifer*, *Rana catesbeiana*, *Rana clamitans*, *Rana palustris*, and *Rana sylvatica*). On the basis of accumulation curves, they proposed that surveys in Rhode Island should be conducted for at least 10 min to have a high probability (>90%) of detecting all species.

In our surveys of central Texas frogs, about 77% of all species were detected in the first 5 min, but 15 min was required to detect >90% of all species known to be present and calling at least once during the 30-min surveys. In 32.3% of our surveys, new species were heard for the first time after the initial 5 min. This indicates that for frogs in our area, call surveys of only 5-min duration will not detect all species present and calling in a substantial proportion of the surveys. Compar-

TABLE 1. Summary statistics for temporal and physical conditions during surveys used to study detection efficiency for number of species ($N = 90$), number of *Acris crepitans* ($N = 47$), and number of *Rana sphenocephala* ($N = 40$).

Variable	No. of species	No. *A. crepitans*	No. of *R. sphenocephala*
	Mean, SD (Range)	Mean, SD (Range)	Mean, SD (Range)
Date (days since 1 January)	106, 35 (26–191)	122, 30 (66–191)	96, 29 (49–177)
Time at start of survey (min after midnight)	1299, 52 (1190–1410)	1298, 52 (1199–1395)	1298, 51 (1190–1410)
Air temperature at start of survey (°C)	18, 5 (8–35)	19, 5 (8–35)	17, 5 (8–29)
Water temperature at end of survey (°C)	20, 4 (13–35)	21, 4 (16–35)	19, 3 (14–27)
Cloud cover at start of survey (%)	48, 44 (0–100)	44, 45 (0–100)	42, 43 (0–100)

TABLE 2. Results of general linear model analyses of detection efficiency for number of species ($N = 90$), number of *Acris crepitans* ($N = 47$), and number of *Rana sphenocephala* ($N = 40$).

Explanatory variable	No. of species		No. *A. crepitans*		No. of *R. sphenocephala*	
	F	*P*	*F*	*P*	*F*	*P*
Location	1.18	0.317	1.55	0.188	1.19	0.352
Year	2.89	0.042	2.04	0.133	0.76	0.529
Wind force at start of survey	0.23	0.796	0.84	0.444	1.11	0.347
Survey duration	4.17	0.020	0.02	0.978	1.01	0.381
Date	0.19	0.661	2.53	0.124	0.00	0.989
Time at start of survey	0.03	0.853	0.00	0.989	4.30	0.051
Air temperature at start of survey	0.18	0.669	0.21	0.652	1.43	0.245
Water temperature at end of survey	0.01	0.931	0.57	0.455	1.09	0.309
Cloud cover at start of survey	1.86	0.177	0.17	0.682	0.10	0.753

ison of our results with those of Shirose et al. (1997) and Crouch and Paton (2002) suggests that cumulative detection efficiency will likely vary with the abundance and calling behavior of the particular frog species in an area.

Influence of Survey Duration.—Summary statistics for explanatory variables indicated that surveys were conducted under a variety of conditions at many locations. The three detection efficiency variables we studied were not influenced significantly by most explanatory variables, including survey date, time, location, wind speed, air temperature, water temperature, and cloud cover. This does not mean that presence and calling frequency of frogs were unaffected by these variables but, rather, that our ability to detect frogs, when present and calling, was not influenced by these variables. Surveys conducted within the range of conditions involved in our analyses are likely to result in similar detection efficiencies for frog species we studied.

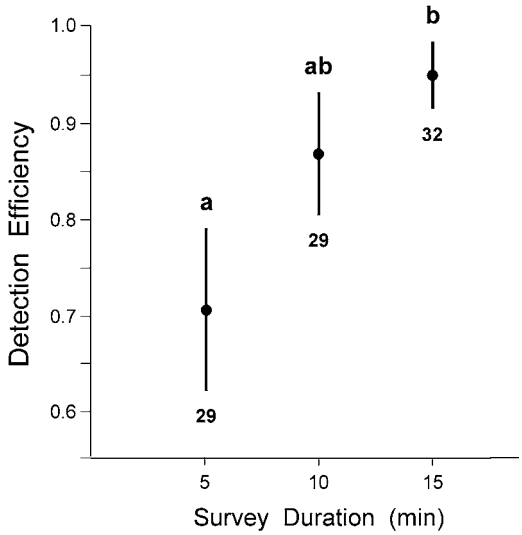

FIG. 2. Detection efficiency for number of frog species for 5-, 10-, and 15-min surveys. Survey durations not marked with a common letter had significantly different detection efficiencies. Means (dots), ±1 SE (lines), and sample sizes (numbers) are presented. Detection efficiency ranged from 0.0–1.0 for all survey durations.

We found a significant effect of survey duration on detection efficiency for number of species; this detection efficiency also was influenced by year in which the survey was conducted. The significant year effect may have occurred because different observers were involved in different years. However, because all investigators used the same techniques, and one investigator was involved in most of the surveys, this possibility is unlikely. Yearly differences in detection efficiency may reflect interannual differences in species detected, differences in calling behavior associated with interannual differences in frog densities, or both. Although the cause of the year effect is unclear, we controlled for year through our analysis. Thus, year did not cloud inferences about the effects of survey duration or other explanatory variables. The year effect emphasizes that detection efficiency may vary among years and that identification of optimal conditions for auditory detection of number of species should be based on multiple years of data.

Our results demonstrate that significantly more species were detected with a 15-min survey (95% of all species) than with a 5-min survey (71% of all species). Compared to 5- and 15-min surveys, 10-min surveys provided results with intermediate efficiency (87%) and precision (Fig. 2). It is important to note that these detection efficiencies are averages based on different species, dates, times, locations, and physical conditions. Some species, such as *A. crepitans*, call frequently and continuously, whereas other species like *P. streckeri* call much more sporadically. Continuously calling species can often be

detected with only a few minutes of listening, but more sporadic callers are likely to be missed in surveys of short duration.

For some studies, the precision of detection efficiency may be of much interest. In this regard, we note that our results suggest a pattern of decreasing variation in detection efficiency with surveys of longer duration, as evidenced by the decreasing standard errors of detection efficiency with increasing survey duration (Figs. 1, 2). The likely reason for this result is that in many surveys of longer duration, 100% of the species present and calling are detected, which decreases the variation in estimates among surveys.

We recognize some of the practical limitations of auditory surveys that use volunteer observers. The amount of time volunteers are willing to listen at a single site may be limited, and increasing the duration of listening time at each site may reduce the number of sites that can be visited on a given night. Increasing listening time also may reduce volunteer retention, which may increase year-to-year variation in observations. These are important factors that must be considered when designing auditory surveys based on volunteer observers.

Shorter surveys are less time consuming and increase the number of sites that can be visited during a given evening, thereby increasing sample size and statistical power; longer surveys increase efficiency and precision. In our study, detection efficiency for number of frog species did not differ between 5- and 10-min surveys; thus, if sampling time is limited and detection efficiency near 0.70 is acceptable, 5-min surveys may be adequate. The higher number of sites that could be surveyed with 5-min surveys versus 10- or 15-min surveys may increase sample size and hence statistical power enough to offset the loss of precision and efficiency associated with 5-min surveys. We recommend that investigators conducting frog call surveys for number of species first determine detection efficiencies using the methods described here and then establish survey durations based on the desired magnitude and precision of detection efficiency and the sample sizes needed to ensure adequate statistical power.

We did not detect significant effects of survey duration on detection efficiency for number of *A. crepitans* or *R. sphenocephala*. This lack of influence may be somewhat surprising—one might expect that, if frogs were calling sporadically, detection efficiency would be higher with longer listening periods. The absence of an effect for particular species in the present analysis may reflect that we were only able to examine this relationship for *A. crepitans* and *R. sphenocephala*, two species that tend to call continuously in our study area. However, Shirose et al. (1997) examined how estimates of calling intensity varied among different investigators who visited the same sites on the same night. They found that increasing survey duration from 3 to 5 min did not significantly increase agreement among different investigators' assessments of calling intensity, which is consistent with our finding of no increase in detection efficiency for number of individual frogs with increasing survey duration.

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Nomenclatural Status of the Synonyms of *Hyla pardalis* Spix, 1824, and Taxonomic Position of *Hyla biobeba* Bokermann and Sazima, 1974 (Anura: Hylidae)

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ABSTRACT.—**The nomenclatural status of the synonyms of *Hyla pardalis* Spix, 1824, is reevaluated, the synonymy of *Hyla* (*Lophopus*) *corticalis* Burmeister, 1856, is supported, and *Hyla rubropunctata* Lutz, 1973 (nomen nudum), is synonymized with *H. pardalis*. *Hyla lundii* Burmeister, 1856, previously in the synonymy of *H. pardalis*, is revalidated. *Hyla pustulosa* Reinhardt and Lütken, 1862, and *Hyllela punctatissima* Reinhardt and Lütken, 1862, previously synonyms of *H. pardalis*, are transferred to the synonymy of *H. lundii*. *Hyla biobeba* Bokermann and Sazima, 1974, is synonymized with *H. lundii*. Diagnoses and comparisons with the members of the *Hyla boans* species group are provided for *H. pardalis* and *H. lundii*, and their geographical distributions are described. The type locality of *H. pardalis* is discussed and reallocated.**

The taxonomic status of many specific names of hylid frogs described from Brazil in the last two centuries have been overlooked. The causes for this are varied but a major reason is the incorrect synonymization of names at earlier times and the subsequent maintenance of these mistakes in modern accounts and catalogs. In this paper we examine the nomenclatural status of names currently referred to the synonymy of *Hyla pardalis* Spix, 1824 (see Lutz, 1973; Duellman, 1977; Frost, 2002) and the taxonomic position of *Hyla biobeba* Bokermann and Sazima, 1974; both species currently are included in the *Hyla boans* group.

The *H. boans* species group contains the following taxa (Frost, 2002): *H. boans* (Linnaeus, 1758), *Hyla faber* Wied-Neuwied, 1821; *Hyla crepitans* Wied-Neuwied, 1824; *H.* pardalis Spix, 1824; *Hyla pugnax* Schmidt, 1857; *Hyla rosenbergi* Boulenger, 1899; and *Hyla wavrini* Parker, 1936. *Hyla biobeba* Bokermann and Sazima, 1974, was included in the group by Martins and Haddad (1988). Species in the group share the following combination of characters: (1) medium to large size (combined snout–vent length, 30.0–120.0 mm); (2) color on dorsum ranging from pale to dark brown, commonly with dark brown X-shaped marks; (3) sides of body with transverse dark brown bars continuous with the dorsal pattern and bifurcating ventrally; (4) posterior surfaces of thighs with ventrally bifurcated vertical dark brown bars; (5) forearm hypertrophied in adult males; (6) humeral crest poorly developed; (7) prepollex well developed, curved, pointed, not bifid; (8) construction or utilization of special sites (nests) for egg laying (as reported for *H. pardalis* by B. Lutz, 1960a; *H. faber* by B. Lutz, 1960b,c, 1961, and Martins and Haddad, 1988; *H. boans* by Duellman, 1970, 2001, and Crump, 1974; *H. rosenbergi* by Breder, 1946, and Kluge, 1981; *Hyla wavrini* by Martins and Moreira, 1991; *H. crepitans* by Caldwell, 1992; *H. biobeba* by Cais, 1992; there is no evidence of constructed nests by *H. pugnax* according to Duellman, 2001).

MATERIALS AND METHODS

Specimens examined are in the following Brazilian collections: MNRJ (Museu Nacional, Rio de Janeiro, State of Rio de Janeiro), MZUSP (Museu de Zoologia, Universidade de São Paulo, State of São Paulo), MZUFV (Museu de Zoologia João Moojen de Oliveira, Universidade Federal de Viçosa, State of Minas Gerais), MCN-AM (Museu de Ciências, Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, State of Minas Gerais), MBML (Museu de Biologia Prof. Mello Leitão, Santa Teresa, State of Espírito Santo), ZUEC (Museu de História Natural, Universidade Estadual de Campinas, State of São Paulo), SJRP (Departamento de Zoologia, Universidade Estadual Paulista, São José do Rio Preto, State of São Paulo), AL-MN (Adolpho Lutz Collection, deposited in MNRJ), CFBH (Célio F.

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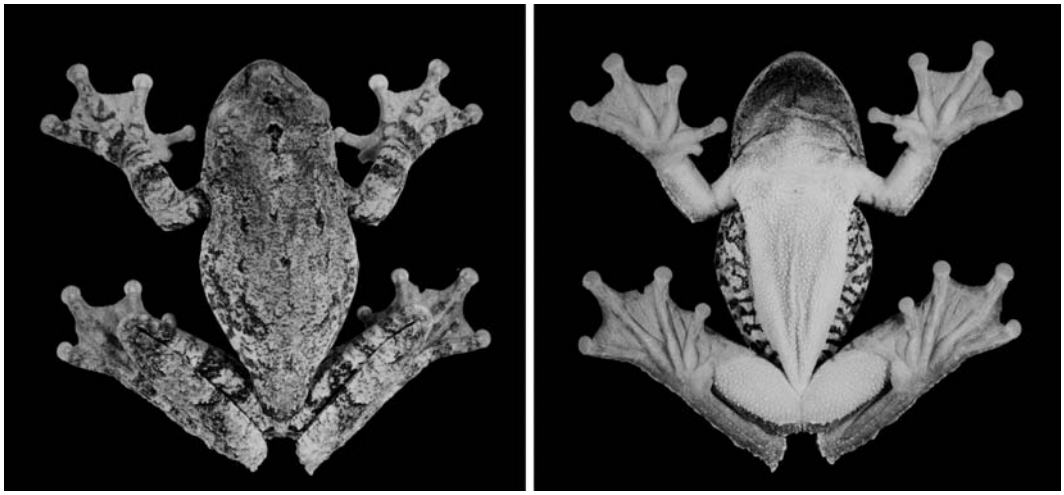

FIG. 1. Dorsal and ventral views of *Hyla pardalis* (MNRJ 24761; SVL 61.4 mm).

B. Haddad Collection, housed in the Departamento de Zoologia, Universidade Estadual Paulista, Campus de Rio Claro, State of São Paulo), EI (Eugenio Izecksohn Collection, housed in the Departamento de Biologia Animal, Universidade Federal Rural do Rio de Janeiro, Seropédica, State of Rio de Janeiro), and WCAB (Werner C. A. Bokermann Collection, deposited in MZUSP). Specimens examined are listed in Appendix 1.

Measurements of SVL (snout–vent length) are in millimeters. Webbing formula notation follows Savage and Heyer (1967) as modified by Myers and Duellman (1982). Line art drawings were made with the aid of a stereomicroscope Zeiss SV-4 equipped with a camera lucida.

RESULTS

Nomenclatural Status of Synonyms of Hyla pardalis Spix, 1824

Hyla pardalis.—The species was described by Spix (1824) based on two syntypes collected in "Provincia Rio de Janeiro." These types are lost (for discussion, see Hoogmoed and Gruber, 1983). The species is perfectly recognizable, occurring in the region of the Atlantic Rain Forest of eastern Brazil, in the states of Minas Gerais, Espírito Santo, Rio de Janeiro, and São Paulo.

Hyla (Lophopus) corticalis.—The species was described by Burmeister (1856) based on not designated types obtained in Nova Friburgo, State of Rio de Janeiro, Brazil. Cochran (1955) synonymized *H.* (*Lophopus*) *corticalis* Burmeister, 1856, with *H. pardalis*. The extensive, detailed original description associated with excellent figures, and the type locality of the species, where *H. pardalis* is currently still very common, support the synonymization.

Hyla (Centrotelma) lundii.—The species was described by Burmeister (1856) based on undesignated types obtained in Lagoa Santa, State of Minas Gerais, Brazil. The extensive, detailed original description, the good-quality figures, and the type locality reveals that the synonymization of *H.* (*Centrotelma*) *lundii* with *H. pardalis* proposed by Peters (1872) was a mistake. Both species are easily recognizable (see below), which leads to the necessary revalidation of the former. As the subgenus is a nomenclatural category not employed for the complex and paraphyletic genus *Hyla*, the proper combination for the species is *H. lundii* Burmeister.

Hyla pustulosa.—The species was described by Reinhardt and Lütken (1862) based on one specimen (holotype, ZMUC 1439; Duellman, 1977; Frost, 2002) collected at Lagoa Santa, State of Minas Gerais, Brazil. Peters (1872) synonymized this species with *H. pardalis*, but the same comments given for *H.* (*Centrotelma*) *lundii* are valid in this case. Consequently, *H. pustulosa* Reinhardt and Lütken is moved from the synonymy of *H. pardalis* Spix to the synonymy of *H. lundii* Burmeister.

Hylella punctatissima.—The species was described by Reinhardt and Lütken (1862) based on one specimen (holotype, ZSM R1436; Duellman, 1977; Frost, 2002) obtained in Lagoa Santa, State of Minas Gerais, Brazil. Müller (1922) synonymized this species with *Hyla geographica* Spix, 1824. Although Bokermann (1966, 1968a) had disagreed with this synonymy, it was followed by Duellman (1977) and Frost (2002). However, Lutz (1973) synonymized it with *H. pardalis*. As indicated in the original description and figure, the holotype is clearly a recently metamorphosed specimen; this was confirmed when Lutz (1973) examined the specimen and compared it to young *H. pardalis*. The size of the holotype (SVL 21 mm; Reinhardt and Lütken,

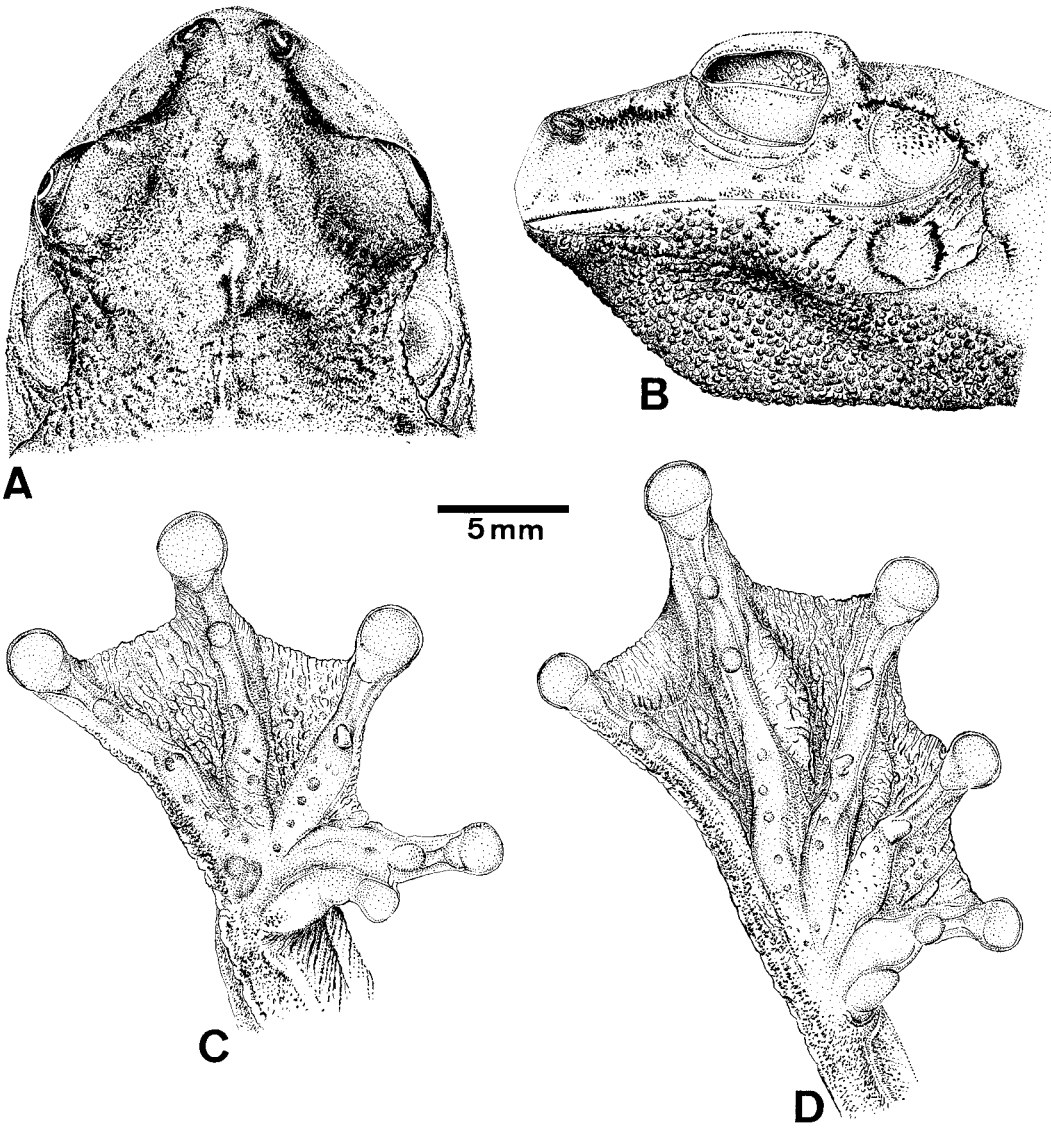

FIG. 2. *Hyla pardalis* (MNRJ 24761): (A) dorsal and (B) lateral views of head; (C) hand; (D) foot.

1862; Bokermann, 1968a), and the characteristic pattern of gray ground color with black dots fits that described for young *H. biobeba* (= *H. lundii*, see below) by Bokermann and Sazima (1974); moreover, this pattern is essentially the same as that described for young *H. pardalis* by Bokermann (1968b) and Lutz (1973). Consequently, *H. punctatissima* Reinhardt and Lütken is here synonymized with *H. lundii* Burmeister.

Hyla rubropunctata.—In her description of the juveniles of *H. pardalis*, Lutz (1973) indicated that these specimens were often seen by her and by her father, A. Lutz, in the Serra da Bocaina and in Petrópolis. She also reported that A. Lutz had a watercolor painted for which he had a manuscript name of *H. rubropunctata*, but he refrained from publishing this name as he strongly suspected that they were young of a larger species. A. Lutz was perfectly correct, but B. Lutz's (1973) publication of the reference name created by her father produced a nomen nudum associated with *H. pardalis*.

Taxonomic Status of Hyla biobeba Bokermann and Sazima, 1974

Hyla biobeba was described by Bokermann and Sazima (1974) on the basis of specimens collected in the Serra do Cipó, Municipality of Jaboticatu-

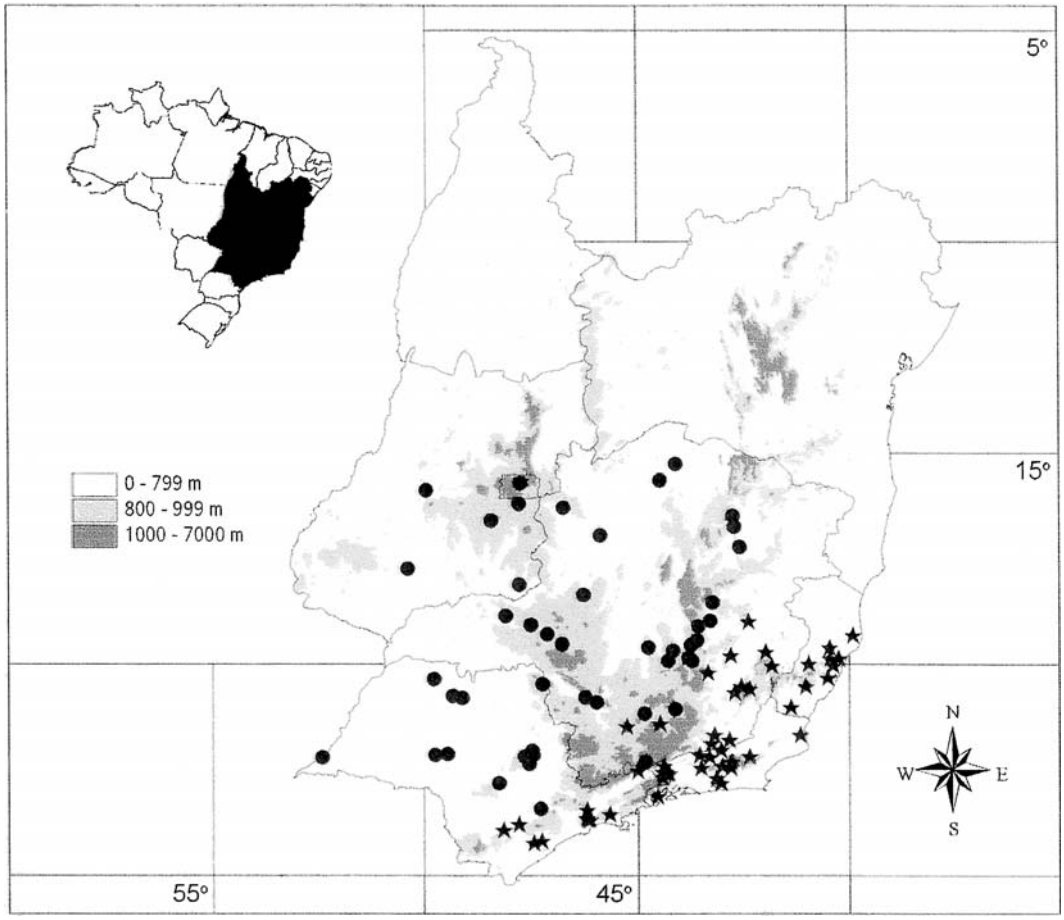

FIG. 3. Geographical distribution of *Hyla pardalis* (stars) and *Hyla lundii* (dots).

bas, State of Minas Gerais, Brazil. The authors placed the species in the *Hyla martinsi–Hyla langei* group, although they reported that the dorsal color pattern much resembled that of *H. pardalis*. Martins and Haddad (1988) considered this species to be in the *H. boans* group, but Duellman (2001) did not follow this assignment.

Hyla lundii Burmeister was described from Lagoa Santa, a locality about 50 km from the Serra do Cipó. Comparison of the original description and figures, and specimens (including topotypes) of *H. lundii* with specimens (including holotype and paratypes) currently identified as *Hyla biobeba* Bokermann and Sazima, 1974, reveal that they are identical, and the latter is a junior synonym of the former.

Hyla pardalis Spix, 1824
Figures 1–2

Hyla pardalis Spix, 1824.
Hyla (*Lophopus*) *corticalis* Burmeister, 1856.
Hypsiboas pardalis-Cope, 1867.
Hyla rubropunctata Lutz, 1973 (nomen nudum) (New synonymy).

Syntypes.—ZSM 2499 (two specimens), currently lost; see Hoogmoed and Gruber (1983) for discussion.

Type Locality.—"Provincia Rio de Janeiro" (Spix, 1824), Brazil, but see below.

Diagnosis.—A member of the *H. boans* species group, characterized by (1) medium size (SVL 48.0–63.0 mm in males, 58.0–70.0 mm in females; Lutz, 1973); (2) dorsum irregularly glandular, giving a rough aspect; (3) dorsal color greenish brown with an irregular pattern of dark brown and gray stains and bars, similar to tree bark or lichens; (4) well-developed undulated or scalloped dermal ridge on outer edge of arms, hands, feet, and toes; (5) cloacal flap and calcar well developed; (6) cloacal region covered by a well defined, glandular plate with lichenous aspect; (7) palmar formula, I 2 ½–2 ⅔ II 1–2^{+} III 1–1 IV; (8) plantar formula, I 1–1 ½ II 1–1 ½ III 1–2 IV 1 ½–1 V.

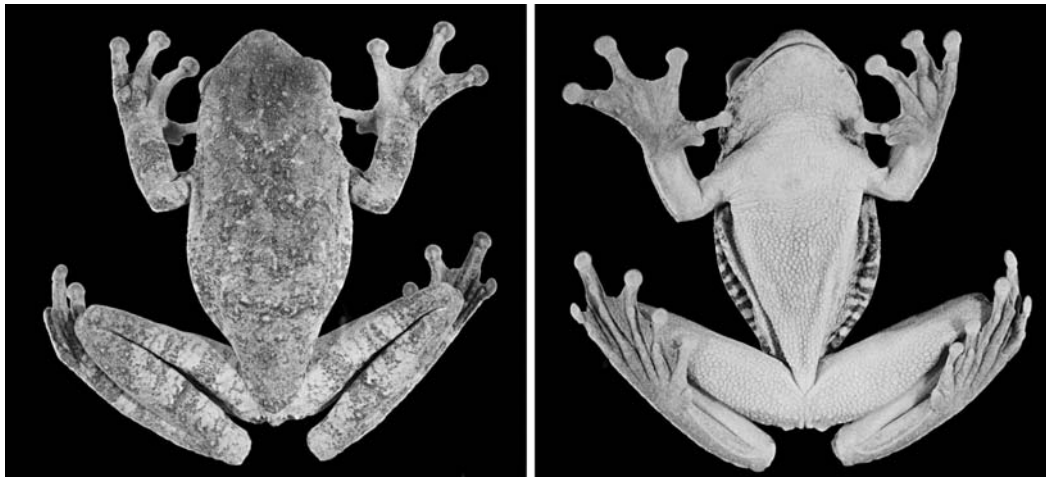

FIG. 4. Dorsal and ventral views of *Hyla lundii* (MNRJ 23970, SVL 67.4 mm).

Comparisons with Other Species.—*Hyla pardalis* is distinguished from all other species of the *H. boans* group, except for *H. lundii*, by the lichenous dorsal pattern (other species uniformly brown, commonly with a middorsal longitudinal dark brown stripe), by the development of dermal ridges (absent in the other species), and by the smaller size (combined SVL 60.0–132.0 mm in males and females of the other species; Lutz, 1973; Kluge, 1981). Additionally, *H. pardalis* is distinguished from *H. boans* and *H. wavrini* by the absence of golden arabesques on the transparent part of the lower eyelid (present in those species), and from *H. faber* and *H. rosenbergi* by the presence of well-developed calcars (absent in those species). The rugose aspect, the presence of dermal ridges, calcars, cloacal flap, and cloacal lichenous plate, and the extensive webbing distinguish *H. pardalis* from *H. crepitans*, *H. lundii*, and *H. pugnax* (dorsal rugosity and dermal ridges, calcars, and cloacal flap poorly developed in *H. lundii*, absent in *H. crepitans* and in *H. pugnax*; cloacal plate absent and hands and feet less webbed in those three species).

Distribution.—Eastern Brazil, in the states of Minas Gerais, Espírito Santo, Rio de Janeiro, and São Paulo (Fig. 3).

Remarks.—Full and good descriptions of the species were provided by Burmeister (1856) as *H.* (*Lophopus*) *corticalis*, and by Cochran (1955). Descriptions of the adult, secondary sex characters, color, pattern, voice and habits, nests and juveniles were presented by Lutz (1973); however, her statements on geographical distribution are incorrect because she combined *H. pardalis* and *H. lundii*. Clay nest construction and spawn were described by Lutz (1960a). Mating call, tadpole, and newly-metamorphosed young were described and figured by Bokermann (1968b). Descriptions and figures of adults, larval morphology, habitat, advertisement call, and ecology were provided by Heyer et al. (1990). The species is recognizable and it is unnecessary to designate a neotype.

The type locality of *H. pardalis* was clearly stated as "Provincia Rio de Janeiro" by Spix (1824) and restricted to the Municipality of Rio de Janeiro (as "Rio de Janeiro, Guanabara"), State of Rio de Janeiro, Brazil, by Bokermann (1966). However, the species does not occur in the Municipality of Rio de Janeiro, as stated by Lutz (1973) and Izecksohn and Carvalho-e-Silva (2001) and supported by our data. Thus, Bokermann's restriction of the type locality must be reevaluated.

In discussing the type localities of the species proposed by Spix, Vanzolini (1981) commented that many of these localities have grown and what was, for example, "near Rio de Janeiro" (as commonly referred by Spix through Latin adverbs *ad, prope*, and *juxta*), are today much nearer the center than the periphery of the city. Another major problem with Spix's localities is the old South American custom of calling a province and its capital by the same name, as in the case of Rio de Janeiro (Vanzolini, 1981). The combination of both circumstances led Bokermann to restrict erroneously Spix's "Provincia Rio de Janeiro" to the current City of Rio de Janeiro.

During their stay in Rio de Janeiro, Spix and Martius did not travel extensively in the province and, as stated by Vanzolini (1981), they cited more species for the province than for the city. They did travel to the farm "Mandioca," owned by Baron Georg Heinrich von Langsdorff (1774–1852), the Russian consul and naturalist, on the slope of the Serra dos Órgãos (Vanzolini, 1981). *Hyla pardalis* occurs there today, and it is likely that Spix obtained his specimens there. Consequently, we change the restriction of the type locality of *H. pardalis* to the former farm

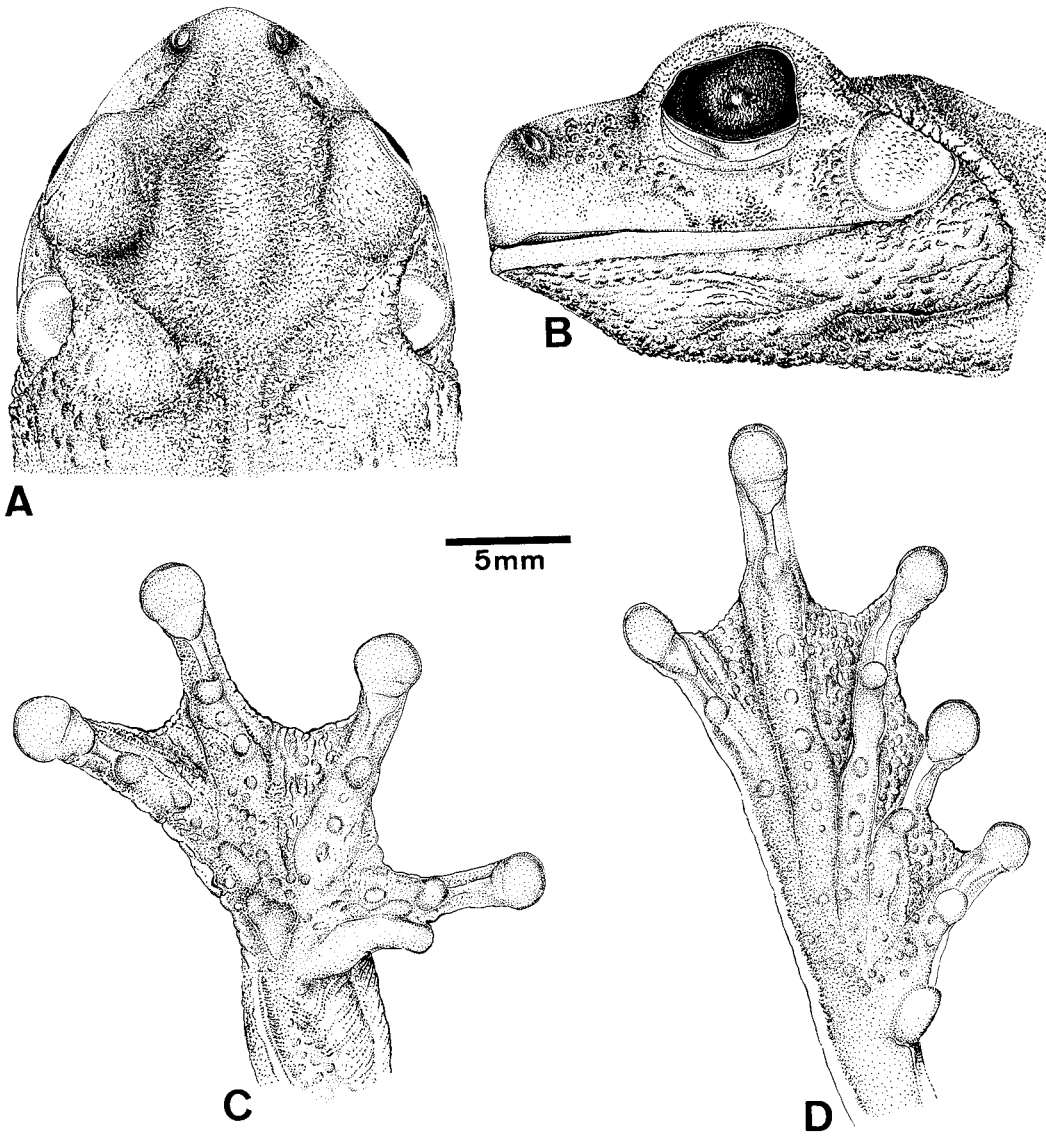

FIG. 5. *Hyla lundii* (MNRJ 23970): (A) dorsal and (B) lateral views of head; (C) hand; (D) foot.

"Mandioca" (approximately 22°35'S, 43°11'W), near the current locality of Santo Aleixo, Municipality of Magé, State of Rio de Janeiro, Brazil.

Hyla lundii Burmeister, 1856 (Revalidated)
Figures 4–5

Hyla (*Centrotelma*) *lundii* Burmeister, 1856.
Hyla pustulosa Reinhardt and Lütken, 1862 (New synonymy).
Hylella punctatissima Reinhardt and Lütken, 1862 (New synonymy).
Hyla biobeba Bokermann and Sazima, 1974 (New synonymy).
Types.—Not designated (Burmeister, 1856).

Type Locality.—Lagoa Santa (19°37'S, 43°53'W), State of Minas Gerais, Brazil.

Diagnosis.—A member of the *H. boans* species group, diagnosed by (1) medium size (SVL 54.0–70.8 mm in males, 54.3–66.1 mm in females; Cais, 1992); (2) dorsum rugose; (3) dorsum grayish brown with a irregular pattern of dark gray stains and bars, similar to tree bark or lichens; (4) undulated dermal ridge on the outer edge of arms, hands, feet, and toes present, poorly developed; (5) cloacal flap and calcar poorly developed; (6) cloacal region not modified; (7) palmar formula, I 3^{+}–$2^{1}/_{3}$ II $1^{1}/_{5}$–2 ½ III 2–2 IV; (8) plantar formula, I $1^{1}/_{5}$–2^{-} II 1–2^{-} III 1 ½–2 ½ IV $2^{1}/_{5}$–1 V.

Comparisons with Other Species.—*Hyla lundii* is distinguished from all other species of the *H. boans* group, except for *H. pardalis*, by the dorsal lichenous pattern (other species uniformly brown, commonly with a middorsal longitudinal dark brown stripe), by the presence of dermal ridges (absent in the other species), and by the smaller size (combined SVL 60.0–132.0 mm in males and females of the other species; Lutz, 1973; Kluge, 1981). Additionally, *H. lundii* is distinguished from *H. boans* and *H. wavrini* by the absence of golden arabesques on the transparent part of the lower eyelid (present in those species), and from *H. faber* and *H. rosenbergi* by the presence of dermal ridges and calcars (absent in those species). From *H. pardalis*, *H. crepitans*, and *H. pugnax* it is distinguished by the rugose lichenous dorsum (rugose in *H. pardalis*, smooth in *H. crepitans* and *H. pugnax*), poorly developed dermal ridges, calcars, and cloacal flap (well developed in *H. pardalis*, absent in *H. crepitans* and *H. pugnax*), webbing less developed and absence of cloacal plate (present in *H. pardalis*, absent in *H. crepitans* and *H. pugnax*).

Distribution.—Central and southeastern Brazil, in the Federal District and states of Goiás, Minas Gerais, and São Paulo (Fig. 3).

Remarks.—Good descriptions and figures of adult, mating call, tadpole, and habits of the species (as *H. biobeba*) were provided by Bokermann and Sazima (1974). The species is easily recognizable and it is unnecessary to designate a neotype.

Discussion

Species of the *H. boans* group exhibit a suite of morphological and behavioral characters unique among hylid frogs. As pointed out by Savage (2002), if this group deserves generic status, *Boana* Gray, 1825 (type-species, *Rana boans* Linnaeus, 1758, by monotypy; Duellman, 2001; Frost, 2002) is the available name.

The group has a broad distribution from Costa Rica, in Middle America, to southern South America east of the Andes (see accounts on distribution of each species in Frost, 2002). However, the distributions of *H. lundii* and *H. pardalis* given by Frost (2002) require modifications based on our data.

Hyla pardalis occurs in eastern Brazil, in the states of Minas Gerais, Rio de Janeiro, and São Paulo, associated with the Tropical Atlantic Domain (for definitions and limits of the Brazilian morphoclimatic domains, see Ab'Saber, 1977). *Hyla lundii* is distributed in central and southeastern Brazil, in the Federal District and states of Goiás, Minas Gerais, and São Paulo, associated with the Cerrados Domain (Ab'Saber, 1977). Both species inhabit clearings, forest borders, and gallery forests along small rivers but do not enter the forest proper. Although in some regions they occur very closely, sympatry has not been documented. This proximity is probably caused by the occurrence of the species in the contact area between both morphoclimatic domains, which they primarily occupy. Contrary to the core areas of each domain, where the morphoclimatic characteristics are fully observed, on the borders there exist indentations of one in another, making possible the geographical, but not ecological, proximity. However, in many localities of northern Minas Gerais, *H. lundii* and *H. crepitans* occur sympatrically, and in many others *H. lundii* or *H. pardalis* occur in sympatry with *H. faber*. However, *H. crepitans* and *H. faber* inhabit primarily open areas and do not occur syntopically with either *H. lundii* or *H. pardalis*.

Hyla lundii and *H. pardalis* are the only members of the *H. boans* group to have the dorsal surfaces of body and limbs irregularly glandular, giving a rough aspect, associated with a color pattern of grayish- to greenish-brown with irregularly distributed stains and bars dark brown or dark gray. This skin texture and color pattern give a lichenous aspect to these frogs, similar to tree bark. This general appearance shared by these species distinguishes them from all other members of the *H. boans* group and may indicate close phylogenetic relationships.

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APPENDIX 1

Specimens Examined

Hyla pardalis.—Brazil: *Minas Gerais*: Caratinga, Fazenda Montes Claros (MNRJ 21885–21886, MZUSP 65261, 65270, MZUFV 1071–1072); Caratinga (ZUEC 6617–6618); Juiz de Fora, Água Limpa (MNRJ 25815, 25818, 25819–25820, AL-MN 132); Juiz de Fora, Torreões (MNRJ 18512); Reserva Biológica de Mar de Espanha (MNRJ 22341); Mar de Espanha (MZUFV 1083); Araponga, Parque Estadual Serra do Brigadeiro (MZUFV 3320–3325, 3682); Pedra do Anta (MZUFV 3646–3651); Varginha (MNRJ 130); Simonésia, Estação Biológica Mata do Sossego (MNRJ 25746); Carrancas (ZUEC 9737); Viçosa (MZUFV 390–392, 417–418, 1233–1235, 1473–1477, 3547–3548, ZUEC 6152–6153); Mariana (MZUSP 1382–1383, 1066, 1225; MZUFV 585–587, AL-MN 96); Belmiro Braga, São José das Três Ilhas (MNRJ 26017); Ouro Preto, Parque Estadual do Itacolomi (MCN-AM 1836–1838); Açucena (MCN-AM 1991–1992); São Domingos do Prata (MCN-AM 1750–1754); no data (MNRJ 2934, 12652). *Espírito Santo*: Rio Doce (MZUSP 2155); Linhares, Sooretama (MZUSP 7794); Santa Teresa (MNRJ 1250, 1369, 1527, 1726, 3329, 7518–7521, 8294–8297, 13882, 26023, MZUSP 34056, MBML 57, 59, 226, 290, 383, 406, 408, 409, 410, 511–514, 631, 677, 1124, WCAB 38605–38606); Santa Teresa, Reserva Biológica de Santa Lúcia (MBML 60, 257, 462, 463, 706, 1184, 1194–1195, 1553); Santa Teresa, Reserva Biológica de Nova Lombardia (MBML 407); Santa Teresa, Barracão (MNRJ 30082–30083); Marechal Flo-

riano/Domingos Martins, Fazenda Floriano (CFBH 1470–1471); Mutum, Fazenda Coutinho (MNRJ 1316); Goytacazes (MNRJ 1452); Afonso Cláudio (MNRJ 25816–25817); Castelo, Forno Grande (MBML 56); Santa Leopoldina, Crubixá-Mirim (MBML 242); Fundão, Parque Municipal do Goiapaba-Açu (MBML 1263–1264); no data (MNRJ 1827, 10171). *Rio de Janeiro*: Rio de Janeiro (MNRJ 129); Petrópolis, Fazenda Inglesa (MNRJ 25740); Petrópolis, Independência (MNRJ 738); Petrópolis, Quitandinha (MNRJ 25808–25811, AL-MN 3923–3924); Petrópolis (MNRJ 2004, AL-MN 1341–1342); Paraty (MNRJ 25741–25743); Três Rios, Areal (MNRJ 25744); Três Rios, Patronato (MNRJ 16078); Engenheiro Paulo de Frontin, Morro Azul (MNRJ 21008, 21674, 21887–21890, 25747, 25749, 25750–25753); Engenheiro Paulo de Frontin, Sacra Família do Tinguá (MNRJ 25771–25772, ZUEC 6328); Nova Friburgo, Macaé de Cima (MNRJ 25805); Nova Friburgo, Cascatinha (MNRJ 25779); Nova Friburgo, Mury (MNRJ 26018–26020); Nova Friburgo (MNRJ 23388–23389, 25825–25827, AL-MN 2681, 2846–2847); Guapimirim (AL-MN 3018–3019); Miguel Pereira (MZUSP 62955); Duque de Caxias, Barro Branco (MNRJ 1454, 1583, 1589, 1644, 2268, 2759, 8069–8070, 8261–8263, 8268–8273, 8494, 25812–25814, MZUSP 118, AL-MN 3216–3218); Duque de Caxias (WCAB 38604); Teresópolis, Alto do Soberbo (MZUSP 53348); Teresópolis, Parque Nacional da Serra dos Órgãos (MNRJ 16682); Teresópolis, Agriões (MNRJ 25829–25831); Teresópolis (MNRJ 127, 209, 643, 5115–5119, 5203–5207, 5732–5742, 16865, 24742–24770, 25748, 25778, 25795–25797, 25832, 25833–25834, WCAB 1780, 38607–38609); Valença (MNRJ 25745, MZUSP 34142); Parque Nacional do Itatiaia (MNRJ 3691, 25824, 25828, MZUSP 10827, 75735, WCAB 19695, 19701–19702). *São Paulo*: Boracéia (MZUSP 1611, 1613, 4075, 4571, 5376, 10375, 10906, 31247–31256, 31257–31267, 37659, 54476, ZUEC 3625, 6050); Fazenda do Bonito, Serra da Bocaina (MZUSP 31268–31269); São José do Barreiro, Serra da Bocaina (ZUEC 6576); Serra da Bocaina (MNRJ 25821, 25822–25823, WCAB 5349); Juquiá, Fazenda Poço Grande (MZUSP 207); Arapeí (ZUEC 6496); Piquete (MZUSP 188, 201); Campo Grande da Serra (MZUSP 225, 76519); Ferraz de Vasconcelos (MZUSP 34476); Rio Grande da Serra (MZUSP 298); São Miguel Arcanjo (MZUSP 76596, 76305); Fazenda Intervales (MZUSP 93277); Paranapiacaba, Campo Grande (WCAB 35984–35989, 35994–35996, 35998–35999, 36291–36298, 36301–36304, 37591); Paranapiacaba, Santo André (ZUEC 6048); BR 2, km 102, Miracatu (WCAB 45139); Formoso, Fazenda Guanabara (AL-MN 891–893).

Hyla lundii.—Brazil: *Minas Gerais*: Serra do Cipó, Usina (MZUSP 74263, holotype of *H. biobeba*, ex-WCAB 46249); Serra do Cipó, km 110 (MZUSP 74303, 73891–73896, paratypes of *H. biobeba*, ex-WCAB 47418, 47557–47562); Serra do Cipó, MG 2, km 105, 1090 m (MZUSP 56880–56882); Jaboticatubas, Serra do Cipó (WCAB 46872, MZUFV 1431, 1618, 2278, SJRP 5421–5422, 5423–5424); Jaboticatubas, Fazenda de Cima (MNRJ 27192); Serra do Cipó, Santana do Riacho, Córrego Chapéu do Sol (CFBH 0770); Conceição do Mato Dentro (ZUEC 2691, 2772, 2790, 2811, 3621, 10909); Esmeraldas (ZUEC 4022); Alpinópolis (ZUEC 3821); Serro (MZUSP 15878); Rio Pandeiros (MZUSP 14191); Riacho da Cruz (MZUSP 14188–14190); Lagoa Santa (MZUSP 33999, SJRP 4751, 5430); Lavras (MZUSP 59218, 52917); Belo Horizonte, Parque das Mangabeiras (MZUFV 207–208, MCN-AM 615–617, 623, 633–634, 1789); Belo Horizonte (WCAB 4457); Carmo do Rio Claro (WCAB 19063); Mateus Leme (MZUFV 1748); Nova Ponte (MZUFV 1928); Unaí (MZUFV 440–452, 935–936); Perdizes, Unidade de Conservação Galheiro (MZUFV 1992–1994, 2083–2085, 2281); Uberlândia (MNRJ 22097–22099); Presidente Olegário, Estação Biológica Vereda Grande (MNRJ 15973, 25785–25786, 25791); Pitangui (MNRJ 2010, 10500); Turmalina, Peixe-Crú (MNRJ 25780); Turmalina, Córrego do Gigante (MNRJ 27258); Grão Mogol, Alegre (MNRJ 25781); Cristália, Fazenda Cabral (MNRJ 25782–25784); São João Del Rey (AL-MN 117–119); Araxá (AL-MN 779); Passa Quatro (AL-MN 495); Brasilândia de Minas (MCN-AM 1766); Nova Lima, RPPN Mata do Jambreiro (MCN-AM 1782, 1869, 1968). *Distrito Federal*: Brasília (MNRJ 2717, 25794). *Goiás*: Goiás Velho (MZUSP 14184–14185); Santa Helena de Goiás, Bauzinho (MZUSP 33830); Catalão (MZUSP 340); Silvânia, EFLEX (MNRJ 17422–17423, 26015–26016, CFBH 2665, 3037); Luziânia (MNRJ 17421). *São Paulo*: Sorocaba (MZUSP 880); Franca (MZUSP 367); Corumbataí (MZUSP 37797); Porto Cabral (MZUSP 1265); Garça (WCAB 13656); Analândia (CFBH 0341, 0342, 0344, ZUEC 10655, SJRP 5266, 5325–5330); Itirapina (ZUEC 5944); Ipeúna (CFBH 1569); Botucatu, Fazenda Lageado (MNRJ 23963–23971, 25773–25777, MZUFV 003–004); Botucatu, Estrada Botucatu-Rubião Júnior (MNRJ 23972–23983); Botucatu (ZUEC 3292, 8533, SJRP 2205); Engenheiro Schimidt (SJRP 1902, 4063); Marília (SJRP 4072–4975); Mirassol (SJRP 1693, 1704, 1867–1869, 1870–1873); Votuporanga (SJRP 1817, 1888).

Hyla boans.—Brazil: *Acre*: Rio Juruá-Mirim, afluente do Rio Juruá (MNRJ 3906,15247). *Amapá*: Serra do Navio (MNRJ 3795, 14816). *Amazonas*: Benjamin Constant, Rio Javari (MNRJ 2562, 11642–11643); Manaus (MNRJ 4554); Rio Solimões, foz do Rio Javari (MNRJ 1740, 9322–9323). *Pará*: Belém (MNRJ 3012); Rio Cuminá, afluente do Rio Trombetas (MNRJ 0142, 5123).

Hyla crepitans.—Brazil: *Bahia*: Caetité (MNRJ 25068-25085). *Minas Gerais*: Berilo (MNRJ 21597–21599); Cristália (MNRJ 21589, 21600–21602); Grão Mogol (MNRJ 15983–15986); Manga (MNRJ 16989–16992, 21876–21884); Minas Novas, Posses (MNRJ 21308–21311); Turmalina, Peixe Cru (MNRJ 21590–21591, 21592–21596).

Hyla faber.—Brazil: *Paraíba*: Mamanguape, Reserva Biológica Guaribas (MNRJ 18053). *Bahia*: Ilhéus (MNRJ 16964); Prado (MNRJ 15999–16002). *Minas Gerais*: São Gonçalo do Rio Abaixo, Peti (MNRJ 21297, 21402, 21403, 21497–21498). *Rio de Janeiro*: Angra dos Reis (MNRJ 0218); Engenheiro Paulo de Frontin, Morro Azul (MNRJ 21635–21639, 21673); Niterói (MNRJ 18516–18517); Santa Maria Madalena (MNRJ 21822); Três Rios, Areal (MNRJ 16981). *São Paulo*: Botucatu, Lageado (MNRJ 19390–19394); Ribeirão Branco (MNRJ 17658–17659).

Hyla wavrini.—Brazil: *Acre*: Rio Branco, Serra do Sal (MNRJ 3094, 3905, 13329, 15246). *Amazonas*: Balbina (MNRJ 16974); Rio Negro (MNRJ 3096). *Mato Grosso*: Chapadão Parecis, Ponte de Pedra (MNRJ 0140, 0141); Xingu, Jacaré (MNRJ 2521, 2548); Rio Culuene, 40 km acima da confluência com o Rio Xingu (MNRJ 2592, 12057-12061). *Pará*: Javari-Acanga, Rio Tapajós, margem esquerda (MNRJ 21891); Tucurí, ilha do Rio Tocantins (MNRJ 16930).