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Leptodactylus caatingae, a new species of frog from eastern Brazil (Amphibia: Anura: Leptodactylidae)

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Abstract.—A new species of frog of the genus *Leptodactylus* is described from eastern Brazil. The new species differs little morphologically from *L. latinasus*, but the advertisement calls are very different. The geographic distribution of *L. latinasus* and the new species, together with the respective levels of differentiation of morphology and call, is mirrored in the species pair *L. bufonius* and *L. troglodytes*. Presumably the same historical event or events lead to differentiation of these species pairs.

In a revision of the *Leptodactylus fuscus* species group (Heyer 1978), *Leptodactylus latinasus* was characterized as having a major distribution pattern in Argentina, Uruguay, and the State of Rio Grande do Sul, Brazil and a few disjunct localities in eastern Brazil. The late Dr. Adão J. Cardoso recorded the advertisement call of a male *L. latinasus* from the State of Bahia in Brazil and brought the recording to the attention of WRH, pointing out that its call was very different from the other known recordings of *L. latinasus* from Argentina and Rio Grande do Sul, Brazil. More recently, FAJ collected a series of specimens of this eastern Brazil form from the fossil sand dune region of Bahia. The purpose of this paper is to describe the eastern Brazilian population currently identified as *L. latinasus* as a new species and provide new field observations for the taxon.

Materials and Methods

All specimens of the new species in the MZUSP, UEFS, and ZUEC collections (museum abbreviations follow Leviton et al. 1985 with UEFS being the Universidade Estadual de Feira de Santana) were borrowed and data were taken from them. Data for *Leptodactylus latinasus* are those used in Heyer (1978) with some additional data for eye-nostril distance, tympanum diameter, and belly patterns (data for these characters were not evaluated in the study published as Heyer 1978).

Measurement data include snout–vent length (SVL), head length, head width, eye-nostril distance, thigh length, shank length, and foot length, following Heyer et al. (1990) except for the eye-nostril distance being measured by calipers as the distance from the anterior corner of the eye to mid-nostril and the tympanum diameter being measured by calipers as the maximum diameter of the tympanum including the annulus.

Measurement data were analyzed using the software program SYSTAT 10 for principal component analysis (Stenson and Wilkinson 2000) and discriminant function analysis (Engelman 2000).

The advertisement call analyzed of the new species is USNM recording 234, cut 1, from Joazeiro, Fazenda Mary, Bahia, Brazil, 7 March 1990, air temperature 26°C, 1910 h, voucher ZUEC 8833, by Adão J. Cardoso. All calls were recorded from the single voucher specimen. Call rate was based on eight samplings of the recording for a total of 396 calls. Other call parameters are evaluated from analysis of 10 calls. For comparative purposes, a recording of *Leptodactylus latinasus,* USNM recording 19, cut 1, from Embarcación, Salta, Argentina, 22 December 1971, air temperature 22°C, time not noted, unvouchered, by W. Ronald Heyer, was analyzed. Call rate was based on three samplings of the recording for a total of 57 calls. Other call parameters are evaluated from analysis of seven calls (non-overlapping calls in a chorus) with filter bandpass settings of 600 and 11,205 Hz.

Advertisement calls were analyzed using Canary 1.2 software (Charif et al. 1995). The calls were digitized at a sample rate of 22,050 Hz, sample size of 16 bits. Call component terminology follows Duellman and Trueb (1986) and Heyer et al. (1990). Call duration was measured from the waveform. Dominant frequency was determined using the spectrum analysis in Canary with settings of analysis resolution filter bandwidth 349.70 Hz, frame length 256 points, grid resolution time 128 points, overlap 50%, frequency 43.07 Hz, FFT size 512 points, window function hamming, amplitude logarithmic, clipping level −80 dB. Minimum and maximum call frequencies were measured from the audiospectrogram display (spectrogram in Canary terminology) using settings of analysis filter bandwidth 174.85 Hz, frame length 512 points, grid resolution 256 points, overlap 50%, frequency 43.07 Hz, FFT size 512 points, window function hamming, amplitude logarithmic, clipping level −80 dB, display style smooth. Call amplitude modulation was evaluated from visual inspection of expanded waveform displays. Harmonics were determined using both expanded wave form displays and power spectrum analysis displays.

Advertisement Calls

The call of the new species is given at an average rate of 160/min. The call duration ranges from 64 to 77 ms. Each call has 7–8 distinct pulses (Fig. 1), given at a rate between 102 to 109 pulses/sec. The dominant frequency for the entire call has two peaks (Fig. 2), the slightly less loud peak ranges from 1072 to 1121 Hz, the loudest peak ranges from 1543 to 1648 Hz. The call is frequency modulated as rising from the beginning of the call to a maximum frequency at about ⅔ the call duration, then slightly falling to the end of the call; the lowest dominant frequency ranges from 934 to 963 Hz, the highest dominant frequency ranges from 1543 to 1648 Hz. There are no indications of harmonic structure in the call. (Fig. 3).

The call of the new species is dramatically different from the call of *Leptodactylus latinasus* in terms of amplitude structure (Fig. 1, distinct pulses present in the new species, absent in *L. latinasus*) and frequencies (Fig. 3, Table 1). The call of the new species from Ibiraba, Brazil sounds very similar to Cardoso's recording from Joazeiro, Brazil, and very different from the calls of Argentinian recordings of *L. latinasus* and *L. fuscus,* another species in the same species group that occurs in some of the same localities as the new species (FAJ, pers. obs.) The differences between the calls of the new species and *L. latinasus* convincingly demonstrate that they represent two distinct species.

Morphology

The following variation occurs in the new species.

Dorsal patterns include well-defined to weakly defined single or double mid-dorsal dark chevrons (as in Heyer 1978, Fig. 1A, C, p. 3), chaotically placed small to medium sized dark markings, or almost uniform. A very interrupted light or dark mid-dorsal pin stripe is present or absent.

Lip stripes range from a light stripe well-

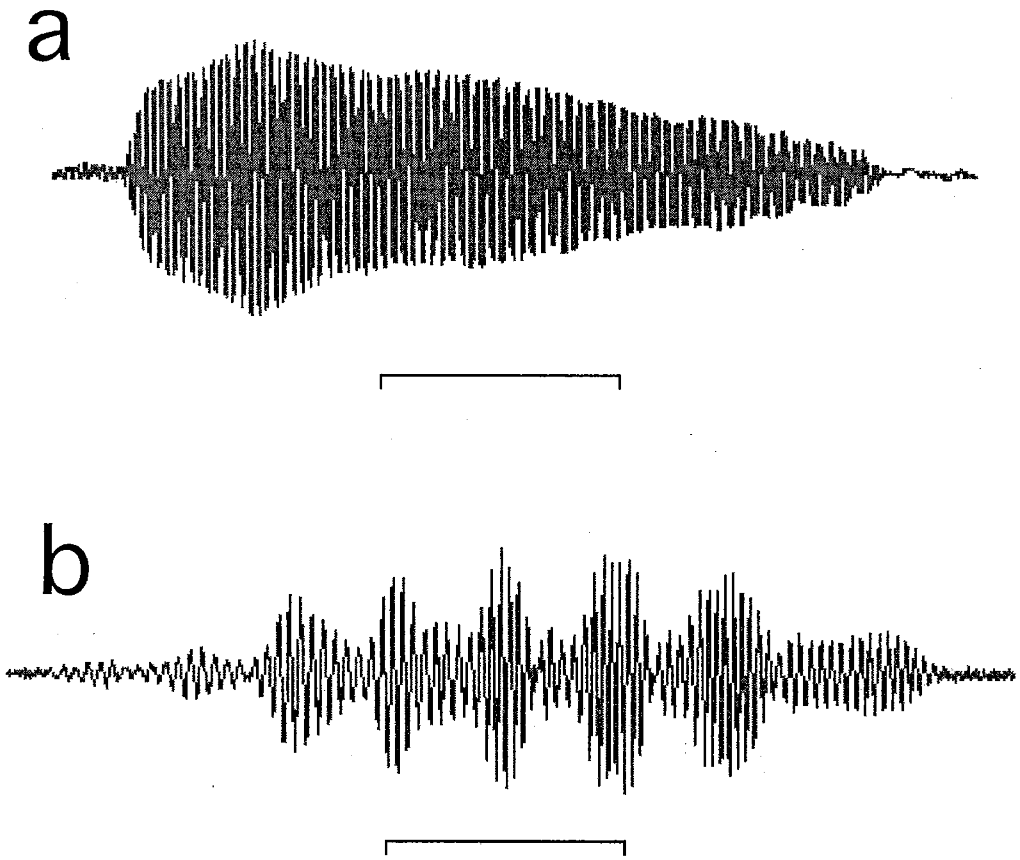

Fig. 1. Wave form of advertisement call of *Leptodactylus latinasus* (a) and the new species from eastern Brazil (b); scale bars = 0.02 sec.

defined both above and below from the tip of the snout passing under the eye and continuing under the tympanum onto the commissural gland to indistinct or indiscernible. All of these conditions occur in specimens from Ibiraba, Bahia; all but one of nine specimens from Itiúba, Bahia have well-defined stripes.

All but one specimen were scored as having a distinct light stripe on the lower face of each posterior thigh surrounded by irregularly shaped broad dark outlines with the rest of posterior thigh having a relatively uniform scattering of melanophores to a mottled pattern. One specimen from Ibiraba, Bahia has a series of light spots, rather than a continuous light stripe.

The upper shanks have irregularly shaped dark transverse bands.

The specimens from Ibiraba, Bahia have a greater development of belly pattern than observed from other localities. The Ibiraba specimens range from having an almost uniform distribution of densely packed melanophores (pale to the eye, but melanophores distinct under magnification), a variegated pattern of melanophores, to groups of melanophores scattered over the belly. Specimens from the other localities either lack a belly pattern, have a weakly variegated pattern of melanophores, or have only a few scattered melanophores lateralmost on the belly.

Many individuals lack any indication of dorsolateral folds. Several individuals have very interrupted folds from the eye to the sacrum. One individual has a very interrupted fold from the eye to the groin. Most

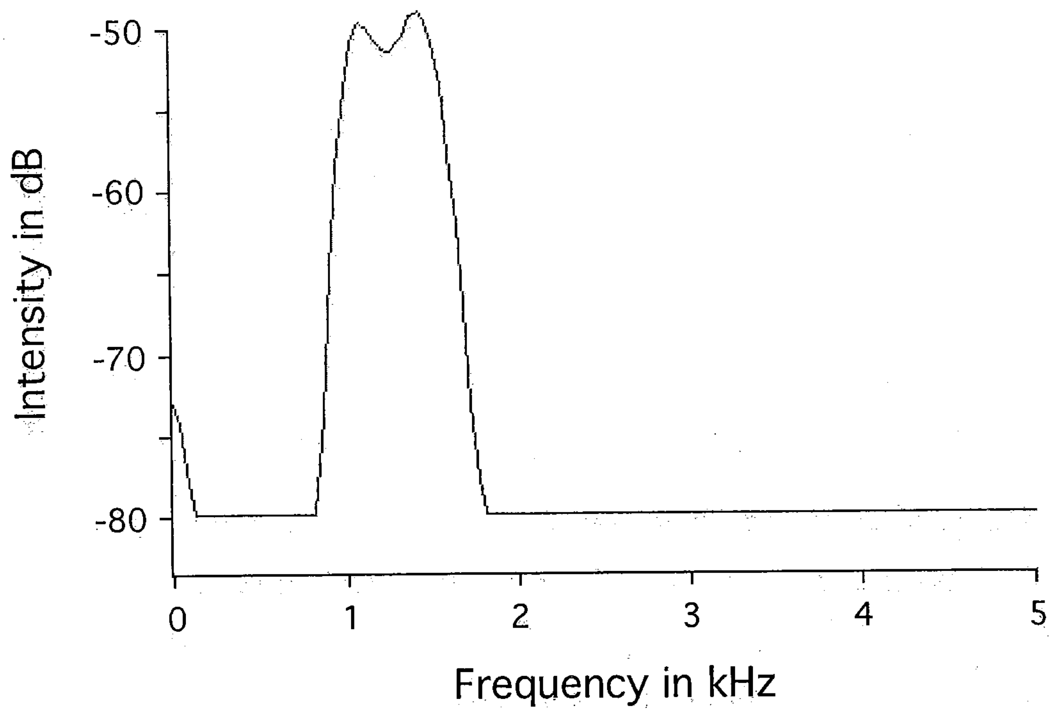

Fig. 2. Power spectrum of advertisement call of new species of *Leptodactylus* from eastern Brazil.

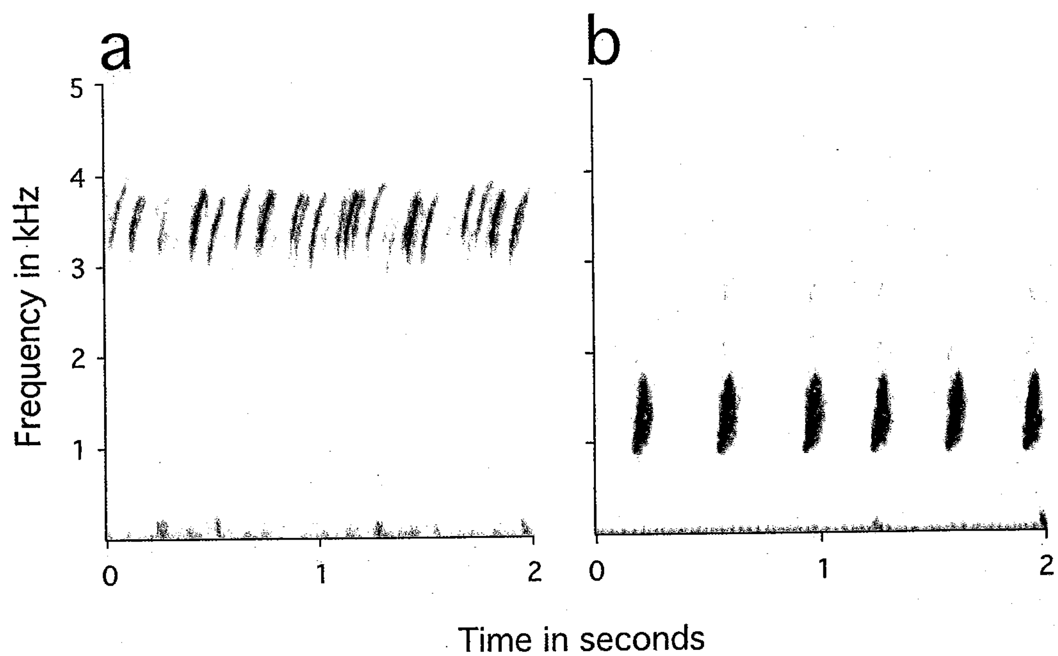

Fig. 3. Audiospectrograms of advertisement calls of *Leptodactylus latinasus* (a) and the new species from eastern Brazil (b).

Table 1.—Advertisement call parameters for *Leptodactylus latinasus* and *L. latinasus*-like specimens from Argentina and Brazil. * indicates data from Barrio (1965). Call data are average values.

Country/state or province	Temperature, celsius	Call rate/min	Call duration/s	Dominant frequency in Hz, entire call	Minimum dominant frequency, Hz	Maximum dominant frequency, Hz
Argentina, Buenos Aires*	26.0	30	0.08[1]		3000	
Argentina, Chaco*	20.0	13	0.09[1]		3500	
Argentina, Salta	22.0	145	0.07	3334	3274	3782
Brazil, Bahia (new species)	26.0	160	0.07	1423	943	1616

[1] Barrio (1965) gave these values as 0.8 and 0.9 s, but his audiospectrograms indicate that the values should be hundredths, not tenths of seconds.

individuals have complete to broken lateral folds.

The upper tibia has scattered to many distinct white tubercles. Twenty of 21 specimens have many distinct white tubercles on the outer tarsal surface and sole of foot. One individual has scattered distinct white tubercles on the outer tarsal surface.

Males range from 32.1 to 36.9 mm SVL (n = 8), females 36.2 and 39.1 mm (n = 2).

The dorsal pattern, lip stripes, posterior thigh pattern, upper shank pattern, mid-dorsal pin stripes, upper shank texture, outer tarsal texture, and sole of foot texture traits are indistinguishable between the new species and *L. latinasus*.

Belly pattern data were not taken for the Heyer (1978) study. WRH examined bellies of all USNM specimens of *L. latinasus* from Argentina, Uruguay, and Rio Grande do Sul, Brazil. Forty-nine individuals lack any belly pattern. One specimen from Argentina (USNM 319587) and two specimens from Uruguay (USNM 535968, 539970) have a few melanophores on the lateralmost venter and/or in the arm insertion portion only of the venter. One individual from Uruguay (USNM 535969) has a pair of small blotches just behind the arm on the sides of the chest. None of the Argentina, Uruguay, or Rio Grande do Sul, Brazil specimens examined have as extensive venter patterns as found in some individuals of the new species.

Body fold development was not scored in the same way for the Heyer (1978) study and this study. A series of 20 well-preserved adult *Leptodactylus latinasus* from Salta Province, Argentina examined for this study shows the same expressions of lateral folds as in the new species, but with different frequencies of occurrences of individual states. Only one of the 20 *L. latinasus* has a very broken dorsolateral fold from the eye to ⅔ distance to the sacrum; the other 19 show no indications of dorsolateral folds. Thus, the new species apparently has a greater frequency of any dorsolateral fold expression than occurs in *L. latinasus.*

There are two sets of measurement data. A more extensive data set (in terms of number of individuals) is available for all adults examined for the Heyer (1978) study for SVL, head length, head width, thigh length, shank length, and foot length. Additional data for eye-nostril distance and tympanum diameter are available for a smaller number of adults for both the new species and *Leptodactylus latinasus.*

Due to the small number of adults available for the new species, principal component analyses are the primary statistical tool used to explore measurement variation in adults of the new species and *Leptodactylus latinasus* (Table 2). The principal component analyses for males show a greater distinction between the two species using the data for all variables versus the data set lacking eye-nostril distance and tympanum diameter data (Fig. 4) than observed in the female data (Fig. 5). The modest differentiation based on measurement data is expected to exceed researcher measurement error, based on previous experience (Hayek et al. 2001). Discriminant function analyses for male data including eye-nostril distance and tympanum diameter data result in 100% correct posterior classification for both the complete data model and backward stepwise model. The discriminant function analyses for the male data lacking eye-nostril distance and tympanum diameter result in 97–98% correct posterior classification of cases for both the complete model and backward stepwise models. Results of multivariate techniques can not be assumed to be generalizable beyond the individual data sets analyzed because any changes in the sample will yield different results to at least some degree (James and McCulloch 1990). Given this caveat, we interpret our results to mean that there is at least some morphological differentiation between the new species and *L. latinasus* that would be confirmed with increased sample sizes.

Overall, the new species and *Leptodac-*

Table 2.—Principal component results, performed with correlation matrices. SVL = Snout-vent length, HL = head length, HW = head width, EN = eye-nostril distance, TD = tympanum diameter, Thigh = thigh length, Shank = shank length, Foot = foot length.

Analyses	Number of specimens	Eigenvalues								% variance explained by components		
		SVL	HL	HW	EN	TD	Thigh	Shank	Foot	1	2	3
Male data, all variables	43	5.45	0.91	0.60	0.41	0.31	0.14	0.11	0.08	68	11	8
Male data, reduced variables	186	4.32	0.73	0.50			0.18	0.14	0.13	72	12	8
Female data, all variables	32	5.13	1.17	0.74	0.40	0.28	0.12	0.09	0.07	64	15	9
Female data, reduced variables	79	4.05	1.19	0.39			0.17	0.13	0.07	67	20	

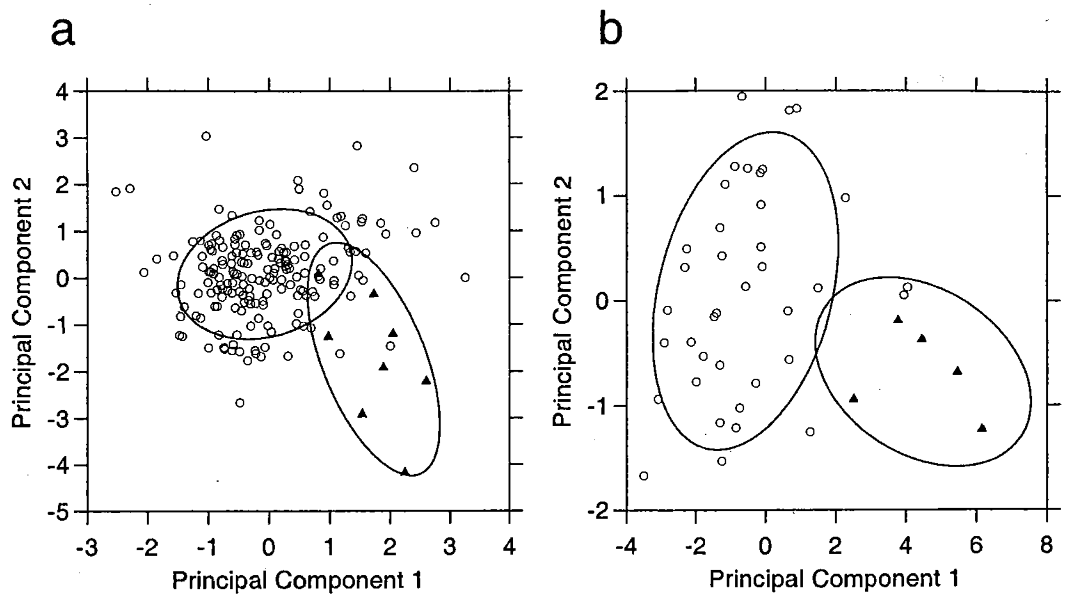

Fig. 4. Male measurement data principal component analyses. A. Reduced variable data set. B. Variable set including eye-nostril distance and tympanum diameter data. Circles = *Leptodactylus latinasus*, filled triangles = new species.

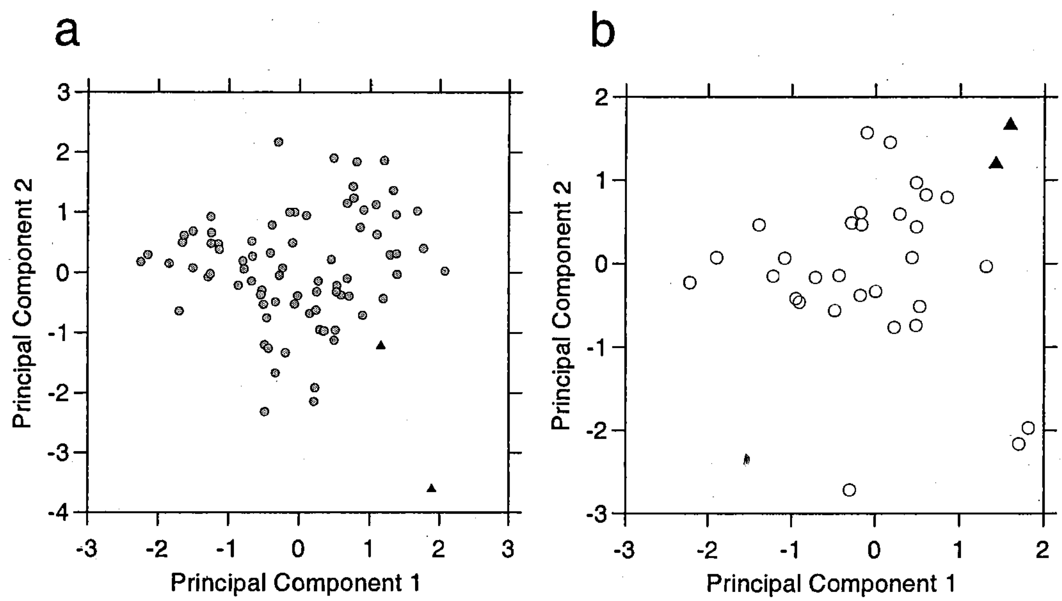

Fig. 5. Female measurement data principal component analyses. A. Reduced variable data set. B. Variable set including eye-nostril distance and tympanum diameter data. Circles = *Leptodactylus latinasus*, triangles = new species.

tylus latinasus are very similar morphologically. There are no characters that completely diagnose the two species. There are a few character states that demonstrate some differentiation between the species. If the only data available were the morphological data, we would interpret the variation to be within-species and would recognize only one species for the two taxa, as was done in the Heyer (1978) study.

Given that the advertisement call data indicate that the specimens from eastern Brazil represent a species distinct from *Leptodactylus latinasus* and there is no name available for it, we hereby describe the taxon lacking a name as:

Leptodactylus caatingae, new species
Figs. 6–7

Holotype.—ZUEC 8833, an adult male from Brazil, Bahia, Joazeiro, 09°25′S, 40°30′W. Collected by Adão J. Cardoso, 7 March 1990.

Referred specimens.—BRAZIL; BAHIA; Bom Jesus da Lapa, 13°15′S, 43°25′W, UMMZ 109991(2); Ibiraba, 10°48′S, 42°50′W, UEFS 686, 688–695; Itiúba, 10°42′S, 39°51′W, MZUSP 38556–38559, 38561–38563, USNM 547844–547845; São José do Rio Grande, 11°49′S, 44°44′W, UMMZ 109992; ESPÍRITO SANTO; São Mateus, 18°44′S, 39°51′W, MCZ A-92142 (recatalogued from the previously lot catalogued specimen MCZ A-1298 cited in Heyer 1978); PERNAMBUCO; Exu, 7°31′S, 39°43′W, MZUSP 51858; Ouricurí, 7°53′S, 40°05′W, MZUSP 77749.

Diagnosis.—The species with a combination of a distinct light stripe on the posterior surface of the thigh and obvious white tubercles on the outer surface of the tarsus and sole of foot in some or all individuals are *Leptodactylus albilabris, caatingae, elenae, fragilis, latinasus,* and *mystaceus. Leptodactylus albilabris* and *mystaceus* have distinct dorsolateral folds (indicated by color pattern in poorly preserved specimens); *L. caatingae* has interrupted, indistinct dorsolateral folds or lacks them. *Leptodactylus caatingae, fragilis,* and *latinasus* have considerable morphological and color pattern overlap and cannot be consistently diagnosed from each other with these characters. The advertisement call of *L. latinasus* is not pulsed and has a high broadcast frequency (3000–3780 Hz); the call of *L. caatingae* is pulsed and has a lower broadcast frequency (940–1620 Hz). The advertisement call of *L. fragilis* is longer (0.19 sec) than the call of *L. caatingae* (0.07 sec). *Leptodactylus caatingae, fragilis,* and *latinasus* have allopatric distributions: *L. fragilis* from southernmost Texas, United States to north coastal Venezuela; *L. caatingae* in eastern Brazil; and *L. latinasus* in southern South America (Argentina, Bolivia, Rio Grande do Sul, Brazil, Uruguay).

Description of holotype.—Snout rounded from above, acutely rounded in profile; canthus rostralis indistinct; lores obtusely convex in cross section; tympanum well defined, moderate size, horizontal diameter about ⅚ eye diameter; vocal slits elongate, parallel to lower jaw, starting about mid-tongue level; vocal sac single with distinct lateral expansions indicated by pronounced folds under lower jaws; vomerine teeth in almost straight line patches separated from each other by about ½ length of a single tooth row, well behind and between almost round choanae; finger lengths II $\approx$ IV $\ll$ I just $<$ III; inner sides of fingers II and III with a line of small tubercular-like projections, otherwise sides of fingers entirely smooth; thumb lacking asperities; snout with distinct flaring ridge; arms not hypertrophied; weakest indications of ulnar ridges; dorsum with small scattered pustular-like warts, lower flanks areolate; supratympanic fold well developed and defined, no other folds discernible; well developed commissural glands, a pair of low, ovoid glands behind tympanum and above posterior arm insertion; ventral disk fold well defined; venter smooth except for areolate ventral thigh surfaces; toe tips IV and V rounded, I, II, III slightly swollen; lateral

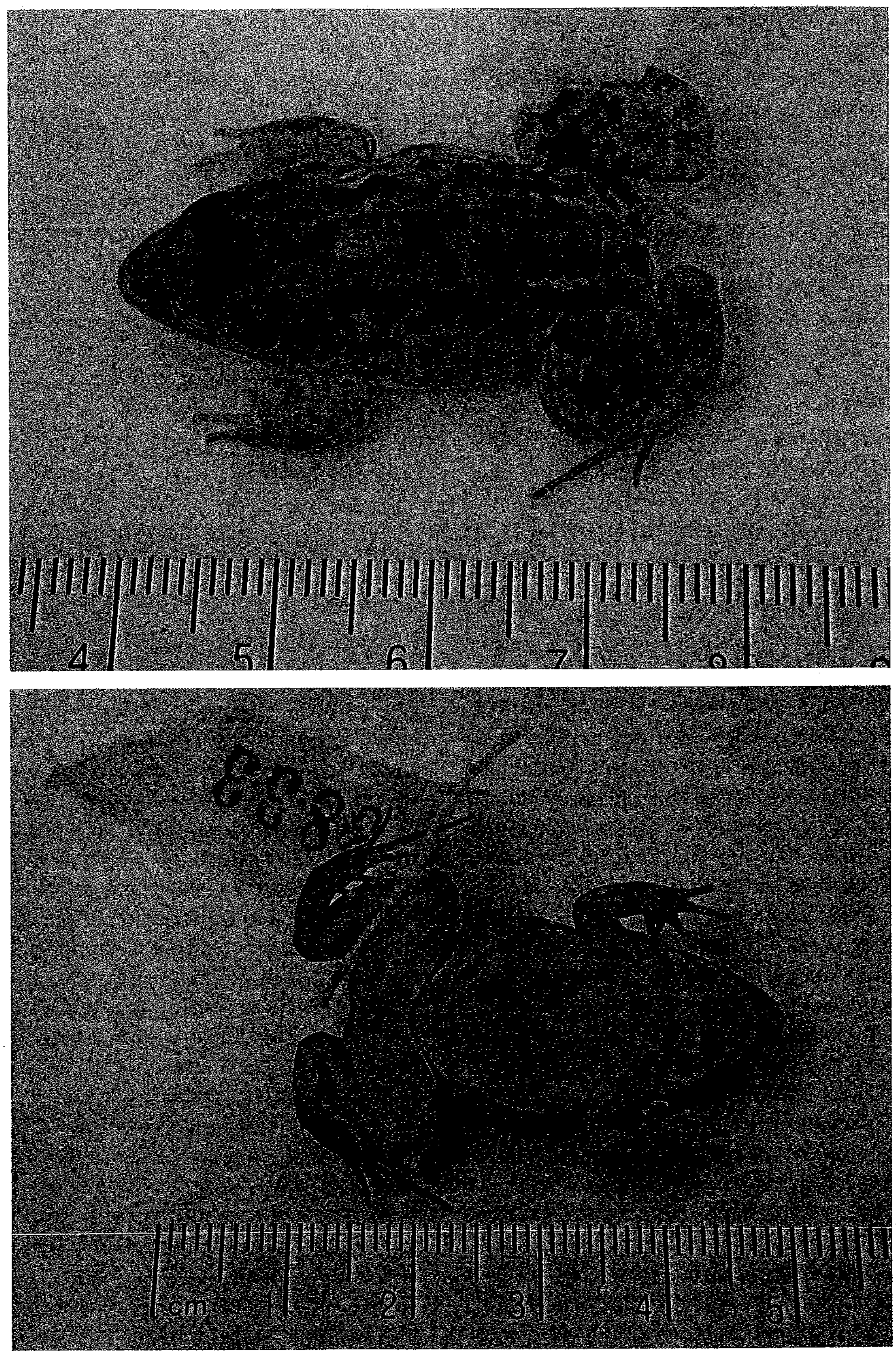

Fig. 6. Holotype of *Leptodactylus caatingae.*

Fig. 7. *Leptodactylus caatingae,* UEFS 695, photo by F. A. Juncá.

toe surfaces lacking ridges or fringes, no indication of basal webbing between toes; subarticular tubercles distinct, pungent; no metatarsal fold; tarsal fold low, broad, glandular, extending $\frac{7}{8}$ distance of tarsus, either abutting inner metatarsal tubercle or with a slight gap between fold and tubercle; upper shank surface with scattered white tubercles; outer tarsal surface with many white tubercles; sole of foot with many white tubercles.

SVL 35.3 mm, head length 14.2 mm, head width 12.7 mm, eye-nostril distance 3.3 mm, tympanum diameter 2.9 mm, femur length 13.4 mm, shank length 14.1 mm, foot length 14.9 mm.

Dorsum blotched tans and browns; a very interrupted series of dark dots from between the nostrils to just past the sacrum; upper limbs with weakly and irregularly defined darker transverse bands; face with dark canthal stripe only well defined just in front of eye; moderately well defined light stripe from tip of snout passing under eye and tympanum and extending to end of commissural gland; flanks with indistinctly darker brown blotches on a tan background; posterior face of thigh with a very distinct light ventral stripe, bordered by dark brown, rest of posterior face of thigh mottled tan and brown; lateral chin area mottled with brown, extending onto vocal folds, rest of venter immaculate.

Etymology.—The name, Latinized from the Portuguese word caatinga, refers to the characteristic distribution of this species within the Caatinga Morphoclimatic Domain (Ab'Sáber 1977).

Larval characteristics.—Unknown.

Advertisement call.—See previous description.

Karyotype.—Unknown.

Distribution.—Currently known from a few localities in eastern Brazil (Fig. 8). All but one of the localities occur in the Caatinga Morphoclimatic Domain (Ab'Sáber 1977). The southernmost locality, in Espirito Santo, occurs in the Atlantic Forest Morphoclimatic Domain (Ab'Sáber 1977). The locality of Rio Grande at São José, Minas Gerais, Brazil for UMMZ 109992 given in Heyer (1978) was incorrect and is São José do Rio Grande, Bahia.

Natural history.—FAJ made the follow-

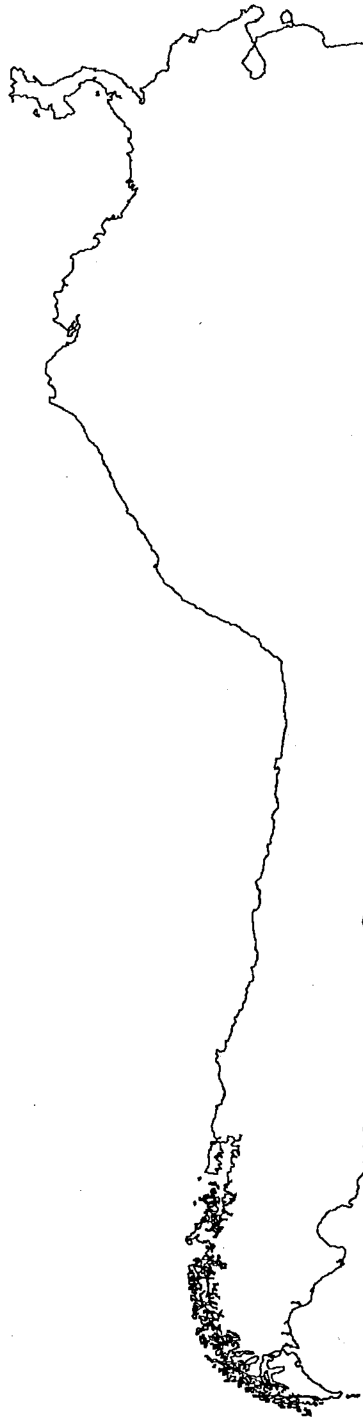

Fig. 8. Distribution map of *Leptodactylus caatingae* and *L. latinasus*. Type locality of *L. caatingae* indicated by dot; other localities by circles. Predicted distribution range of *L. latinasus* indicated by shaded area.

ing observations on specimens from Ibiraba, Bahia. On March 2000, in the rainy season, about 10–20 males were calling within grass bordering a flooded forest area that was totally dry the day before. One of these males was calling in an exposed position and FAJ could observe and collect it. The air temperature was 25°C. Other specimens were collected in pitfall traps, which were put in on one edge of the Icatú River. In that area the vegetation is a typical gallery forest with trees up to 5–7 m tall. In the same area *Leptodactylus fuscus, ocellatus,* and *podicipinus* were calling too. In August 2000 the same area was dry and no individuals of *L. caatingae* were calling, although some *L. podicipinus* males were heard.

Discussion

The call rates of *Leptodactylus latinasus* analyzed for this paper are very different from those analyzed by Barrio (1965, see Table 1) and may impact the call rate described for *L. latinasus* herein. The differences are real and not due to different means of analysis. The major difference between the recordings involved is that Barrio's recordings appear to be of a single calling individual, whereas the recording of *L. latinasus* analyzed herein was a chorus recording, although there seemed to be one primary individual that was louder (i.e., closer to the microphone), but it is possible that two or more individuals were calling equally loudly from the microphone in a manner that their calls did not overlap with each other. Thus, it is possible that the difference in calling rates of *L. latinasus* as presented in Table 1 could be due either to more than one individual actually being analyzed in the Salta recording, or *L. latinasus* increases calling rates when in a chorus of conspecifics. The recorded call of *L. caatingae* has every indication that it is from a single calling male, however.

We are not certain that all of the specimens we have examined of *L. caatingae* represent a single species. There is variation in belly pattern development among specimens of *L. caatingae* from different localities. Advertisement calls are very important in evaluating species limits in the frogs that have been known as *L. latinasus*. Unfortunately, we have only a recording from a single frog of *L. caatingae*. Recordings are needed from the other population samples we have designated as referred specimens of *L. caatingae* in order to determine whether there are additional species contained in the specimens we have examined. Because of the observed belly pattern variation and lack of additional recordings, we think it is inappropriate to designate paratypic specimens for *L. caatingae*.

The currently known distribution of *L. caatingae* is confounding. The Atlantic Forest Morphoclimatic Domain locality of São Mateus, Espírito Santo is peculiar. There are very few species of frogs that occur in both caatinga and Atlantic Forest areas. Copeland Hartt collected MCZ A-92142 in 1865/1866. The available evidence is quite convincing that the specimen was collected from the Atlantic Forest Morphoclimatic Domain and most probably São Mateus itself. Hartt collected amphibians and reptiles from five other localities in addition to São Mateus in the States of Bahia and Espírito Santo. All of these five localities are also from the Atlantic Forest Morphoclimatic Domain. There are no habitat data for MCZ A-92142. There are at least three possibilities to explain a presumably caatinga adapted frog being collected at São Mateus: (1) the São Mateus population inhabits open areas within the Atlantic Forest Morphoclimatic Domain, such as sandy beaches along the ocean coast; (2) the São Mateus population actually represents a new cryptic species of this complex; and (3) this distribution represents another example of how little we really understand about neotropical frog distributions. Collecting new material from São Mateus of *L. caatingae,* including recording its advertisement call, could resolve the current distributional anomaly.

The pattern of differentiation and distribution described herein for *L. caatingae* and *L. latinasus* is very similar to that found between two other members of the same species group (the *L. fuscus* group): *L. bufonius* and *troglodytes.* These two latter species are very similar morphologically and differ markedly in their advertisement calls (Heyer 1978). *Leptodactylus bufonius* has a distribution in the open formations of Argentina, Bolivia, Mato Grosso do Sul, Brazil, and Paraguay. There is an extensive distributional hiatus between *L. bufonius* and *L. troglodytes,* with *L. troglodytes* occurring in open formations of northeast Brazil (compare maps in Figs. 34 and 68 in Heyer [1978]). This similar pattern suggests that the two species pairs shared the same differentiation history, probably the ancestor of each having a general distribution throughout the diagonal of open formations in South America. Whatever event isolated the populations from northeast Brazil from the populations in and adjacent to Argentina was probably the same event that led to speciation of both *L. bufonius–troglodytes* and *L. caatingae–latinasus.* This hypothesis would be corroborated if the levels of molecular differentiation between the pairs of species were identical. If that turns out to be true, the molecular data might provide a suggestion of when the allopatry occurred, which, in turn, might agree with the hypothesis proposed by Vanzolini (1997: 80–84) of separation of dry formation populations by fragmentation due to Pleistocene wet forest expansions during more mesic periods than present.

Acknowledgments

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Literature Cited

Ab'Sáber, A. N. 1977. Os domínios morfoclimáticos na América do Sul. Primeira aproximação.—Geomorfologia (52):1–22 + map.

Barrio, A. 1965. Afinidades del canto nupcial de las especies cavícolas del genero *Leptodactylus* (Anura-Leptodactylidae).—Physis 25:401–410.

Charif, R. A., S. Mitchell, & C. W. Clark. 1995. Canary 1.2 user's manual. Cornell Laboratory of Ornithology, Ithaca, New York, 229 pp.

Duellman, W. E., & L. Trueb. 1986. Biology of amphibians. McGraw-Hill Book Company, New York, St. Louis, San Francisco, 670 pp.

Engelmann, L. 2000. Discriminant analysis. Pp. I-275–I-326 *in* SYSTAT® 10. Statistics I, SPSS Inc., Chicago. 663 pp.

Hayek, L-A. C., W. R. Heyer, & C. Gascon. 2001. Frog morphometrics: a cautionary tale.—Alytes 18: 153–177.

Heyer, W. R. 1978. Systematics of the *fuscus* group of the frog genus *Leptodactylus* (Amphibia, Leptodactylidae).—Natural History Museum of Los Angeles County, Science Bulletin (29):1–85.

Heyer, W. R., A. S. Rand, C. A. G. Cruz, O. L. Peixoto, & C. E. Nelson. 1990. Frogs of Boracéia.—Arquivos de Zoologia 31:231–410.

James, F. C., & C. E. McCulloch. 1990. Multivariate analysis in ecology and systematics: panacea or Pandora's Box?—Annual Review of Ecology and Systematics 21:129–166.

Leviton, A. E., R. H. Gibbs, Jr., E. Heal, & C. E. Dawson. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology.—Copeia 1985:802–832.

Stenson, H., & L. Wilkinson. 2000. Factor analysis. Pp. I-327–I-363 *in* SYSTAT® 10. Statistics I. SPSS Inc., Chicago, 663 pp.

Vanzolini, P. E. 1997. The silvestrii species group of *Amphisbaena,* with the description of two new Brasilian species (Reptilia: Amphisbaenia).—Papéis Avulsos de Zoologia 40:65–85.