

SPECIES IDENTITY IN THE GENUS *ADENOMERA* (ANURA: LEPTODACTYLIDAE) IN SOUTHEASTERN PERU

ARIADNE ANGULO^{1,4}, REGINALD B. COCROFT², AND STEFFEN REICHLÉ³

¹Department of Zoology, Erindale College, University of Toronto, Mississauga, ON, L5L 1C6, Canada

²Division of Biological Sciences, University of Missouri, Columbia, MO 65211, USA

³Fundación Amigos de la Naturaleza, Casilla 2241, Santa Cruz de la Sierra, Bolivia

ABSTRACT: The genus *Adenomera* has been a difficult group for systematic studies because the species are similar and geographically variable. Two species have been reported from the Peruvian Amazon Basin: *Adenomera andreae* and *Adenomera hylaedactyla*. However, acoustic recordings from the Tambopata National Reserve in southeastern Peru reveal four sympatric advertisement call types that are distinctive in acoustic parameters and to the human ear. Some subtle morphological differences are also present. We conclude that there are at least four sympatric species at Tambopata and that *Adenomera* has a greater species diversity than currently acknowledged.

Key words: *Adenomera*; Advertisement calls; Amazon Basin; Call types; Morphs; Sympatry

THE LEPTODACTYLID genus *Adenomera* has long been a puzzle for neotropical field biologists and frog systematists. Heyer's (1973, 1974, 1977) studies have improved the understanding of the taxonomy of *Adenomera*, but more recent data have raised new taxonomic issues, and the identities and relationships of the species still lack resolution. Part of the difficulty can be attributed to considerable intra- and inter-populational morphological variation among most species (de la Riva, 1996). Thus, Heyer (1984; personal communication) suggested that future research efforts should consider other potentially informative characters, such as advertisement calls and karyotypes. Advertisement calls, in particular, can often aid in species identification. Given the importance of advertisement calls in mate recognition (Blair, 1974; Rand, 1985; Ryan, 1983) and their potential importance in speciation (Duellman and Pyles, 1983; Fouquette, 1960), analyses of advertisement calls may be especially useful in resolving the taxonomy of *Adenomera*.

Knowing the reproductive mode could also help in the identification of species. *Adenomera* has the most terrestrial reproductive biology in the Leptodactylinae: eggs are deposited in foam nests away from standing water with tadpoles completing development in the nest (Heyer, 1974). But recently, a second reproductive mode, where eggs are

deposited in foam nests and tadpoles go through an aquatic stage, has also been reported for two species (Almeida and Angulo, 2002; de la Riva, 1995), so knowledge of the reproductive strategies used could potentially help as additional features in species identification.

Seven species of *Adenomera* are currently recognized (de la Riva, 1996; Frost, 2002). *Adenomera andreae* and *A. hylaedactyla* are broadly sympatric in the Amazon Basin and exhibit ecological segregation (Heyer and Maxson, 1982). *Adenomera diptyx*, a recently revalidated species, is known to live in the southernmost border of the Amazon Basin (I. de la Riva, personal communication), occupying more xeric environments than any other *Adenomera* (de la Riva, 1996). *Adenomera lutzi* is known from its type locality, Chinapoon River, Guyana. *Adenomera martinezi* is found in north central Brazil, although it is not clear whether it occurs in an Amazonian or a Cerrado habitat, as the type locality is situated in a transition zone (Bokermann, 1956). *Adenomera bokermanni* and *A. marmorata* are known to occur in sympatry in southeastern Brazil, in Atlantic rainforest environments.

However, the number of species is expected to increase substantially in the next few years, as ongoing research reveals new species formerly confused with currently recognized species, particularly in the Amazon Basin and the Atlantic rainforests of southeastern Brazil (A. Angulo and J. Reichlé, unpublished data;

⁴ CORRESPONDENCE: e-mail, ariadne@zoo.utoronto.ca

Boistel et al., 2003; Kwet and Angulo, 2002). Such is the case in this study.

During three field seasons in the Tambopata National Reserve (TNR) and adjacent buffer zone, southeastern Peru, calls of male *Adenomera* were recorded and voucher specimens collected and preserved. Four distinctive presumed advertisement calls were recorded at more than one locality within the TNR. Using these "call types," it was possible to find certain morphological differences that allowed us to further distinguish these frogs. Herein we analyze the different call types and report on morphological/ecological associations for each specific vocalization. Given the currently changing nature of the group's taxonomy and that it may increase considerably in species number, it is beyond the scope of the present paper to provide a revision of the genus *Adenomera*. Instead, our objectives are to show that there are more kinds of advertisement calls in this group than named species and to pinpoint acoustic and morphological characteristics and habitat associations that could help field workers identify/separate these frogs. This study represents one step toward helping resolve some of the taxonomic issues of this genus.

MATERIALS AND METHODS

Calls of 19 voucher males ($n = 5$ per morph, with the exception of Forest Call III morph, for which four individuals were available) were recorded. Whenever possible, 10 calls were analyzed for every voucher male, with the exception of one specimen (the morph that we have termed Forest Call I) for which only eight calls were recorded. Voucher specimens were deposited at the National Museum of Natural History, Smithsonian Institution, and the Royal Ontario Museum. Other specimens from the same area were also examined to corroborate morphological associations with call types and habitats (see Appendix I for a list of material examined). Type specimens for both *A. andreae* and *A. hylaedactyla* were examined in an attempt to identify the nominal species among the Tambopata specimens.

Field work was conducted during wet seasons (November through March) in 1988–89, 1990, and 1999 at four different sites within the former Tambopata Candamo Reserved

Zone (12° 50' S, 69° 17' W), now Tambopata National Reserve and Bahuaja Sonene National Park in the Department of Madre de Dios, southeastern Peru. The TNR is a protected area of lowland Amazon rainforest covering 274,960 ha (R. Rivas, personal communication) (see Fig. 1 for location of sites).

Vocalizations were recorded with either a Sony TCD-5M tape recorder and a Sennheiser ME-80 microphone or a Sony Walkman Professional WM D6C tape recorder and a Sony ECM-907 microphone. Details of date, time, temperature, weather conditions, habitat, and calling context were noted for every vouchered male (Appendix I). Playbacks of a male's own call type were sometimes used to encourage a shy individual to continue calling.

Calls were analyzed using the Macintosh-based digital signal analysis program, Signalyze 3.12 (Keller, 1994). Sampling frequency rate was set at 44.1 kHz and 16-bit precision. Call figures of temporal and spectral features of calls were produced using a combination of a PC-based sound analysis program, DADiSP, and Signalyze 3.12, and later edited with Corel Draw.

Eleven call parameters were used to describe advertisement calls: call length, call rate, call rise time, pulse rate, number of pulses per call, pulse rise time, pulse duty cycle, dominant frequency, fundamental frequency, other frequencies, and frequency modulation (change in dominant frequency). Terminology for call variables follows Cocroft and Ryan (1995) except for fundamental frequency, which is taken from Duellman and Pyles (1983), and change in dominant frequency, which is taken from Márquez et al. (1995). Other frequencies are defined as those possessing appreciable energy (normally harmonically-related frequencies). Pulse duty cycle is defined as pulse duration divided by pulse period. Frequency information measurements were taken at peak amplitude of each signal. Sample sizes of each call type do not allow for temperature correction using regressions, so temperature ranges are indicated for each call type.

Morphometric features of voucher specimens were measured (in mm) with either an electronic caliper or with an ocular micrometer fitted to a stereoscopic microscope. Measurements were taken as per Heyer et al. (1990). The following measurements were taken with

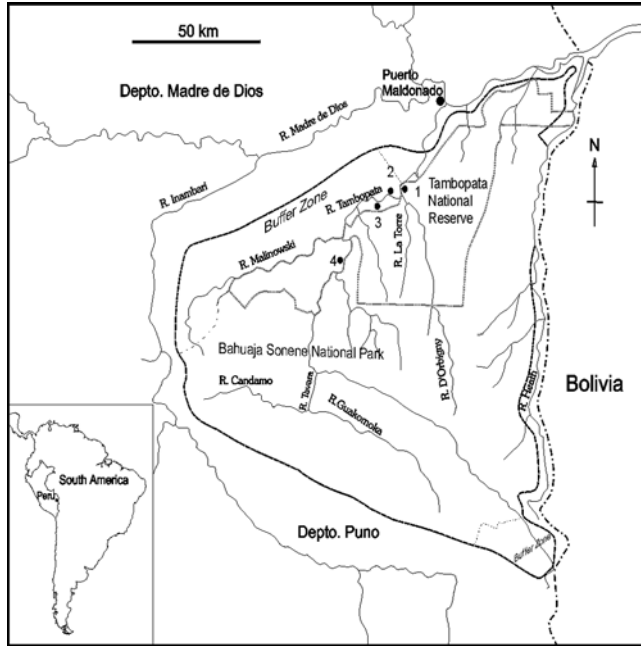


FIG. 1.—Map of the Tambopata National Reserve, Departamento de Madre de Dios, Peru, and surrounding areas. Numbered black circles indicate the following localities: 1 = Explorer's Inn, 2 = Bahuaja Lodge, 3 = Sachavacayoc Centre, and 4 = Tambopata Research Centre (TRC). Modified from Hill and Foody (1994).

the ocular micrometer: head width, head length, eye/nostril distance, thigh length, shank length, tarsus length, foot length, eye diameter, tympanic diameter, forearm length, and hand length. Snout-vent length (SVL) was measured with digital calipers. Specimens were also examined for general external morphological differences (e.g., toe tip shapes, dorsal patterns, supra-tympanum markings, snout and head shape, space between vomerine teeth).

In order to evaluate whether both morphometric and call data distinguish four groups, we used a principal components analysis (PCA), which was performed on the correlation matrix using the untransformed data and using the "varimax" rotation method. In the case of advertisement call data, we have restricted the analysis to the three call types that share a pulsed component. As Forest Call III is qualitatively different (it does not possess perceptible pulses), we have not included it in this analysis.

RESULTS

Four different call types were heard and recorded, and subtle (though sometimes over-

lapping) morphological differences were found among frogs possessing each call type. Table 1 provides a summary of acoustic parameters for the four different call types, and Table 2 provides some morphometric measurements of voucher specimens in addition to the characteristic toe tip shape. Figures 2–5 depict oscillograms, spectra, and spectrograms for each call type. Because of the discrepancy between number of call types and number of described species, we have described all four call types and compared them with those previously reported for *Adenomera*.

Call Types

One call type described herein was compared to data reported in the literature, and we concluded it to be the call of *A. hylaedactyla*. However, given that there are more call types than nominal species available and that we do not know with certainty which are the calls of the nominal species, we have simply named the other types as Forest Calls I–III. Following is a description of the four call types recorded sympatrically (two were recorded syntopically—Forest Calls I and II) in the TNR.

TABLE 1.—Summary of acoustic parameters for all four Tambopata call types. Numbers linked by a hyphen are ranges; all other values are means. Call rate is expressed as calls per minute, and pulse rate is expressed as pulses per second. Abbreviations are as follows: Fund freq = fundamental frequency, dom freq = dominant frequency, other freq = other frequencies, change in dom freq = change in dominant frequency.

Call type	<i>n</i> (frogs)	<i>n</i> (calls)	Temp (C)	Call length (ms)	Call rise time (ms)	Call rate (calls/min)	Pulses/call	Pulse rate (/s)	Pulse duty cycle	Pulse rise time (ms)	Fund freq (Hz)	Dom freq (Hz)	Other freq (Hz)	Change in dom freq (Hz)	
Forest type I	5	48	22.2–26	208.50	34.92	12	20–39	164.40	1	2.48	2375.29	4771.10	6891.65	1151.33	
				155.50–	17.66–	6–36	126.4–242	—	1.05–4.39	2128.40–	4415.90–	6126.60–	429.68–		
				259.25	59.68	—	—	—	2585.90	5052.40	7614.40	1636.52			
Forest type II	5	50	22–23.2	281.35	153.78	22.8	10–17	45.9	0.5	3.03	2213.54	4520.93	6450.23	366.10	
				191.98–	44.89–	15–31.2	28.7–70.2	—	1.02–6.11	2028.90–	4057.90–	5171.80–	–429.68–		
				505.75	227.91	—	—	—	2466.5	4953	7399.60	859.38			
Forest type III	4	40	25.9–26.6	48.61	10.14	52.22	1	—	—	—	2506.70	5106.58	—	811.97	
				37.05–	5.61–	48–60	—	—	—	2208–	4654.6–	—	—	—	515.62–
				89.98	18.09	—	—	—	2679.5	5338.8	1375				
<i>Adenomera hylaedactyla</i>	5	50	24.2–27	46.02	11.26	210	4–6	130	1	4.29	2069.11	4248.43	6146.48	1057.04	
				34.77–	0.84–	162–252	80.4–153.5	—	2.11–5.93	1949.4–	3958.4–	5728.8–	687.5–		
				62.27	22	—	—	—	2208	4475.6	6743.2	1632.81			

Forest Call I (Fig. 2).—This call is a relatively long signal (mean duration 208.50 ms) compared to the other call types reported here and to other *Adenomera* calls (A. Angulo, unpublished data; Angulo and Icochea, 2003). The call rate is relatively low (6–36 calls/min), a feature it shares with the other forest call types. The call is a train of 20–39 pulses and is audibly pulsed to the human ear (although at greater distances the signal is degraded and the pulses are not always distinguishable). Call rise time is very short, and calling onset is abrupt, with an initial high amplitude followed by a lower amplitude for the ensuing pulses. The dominant frequency (4415.90–5052.40 Hz) is approximately twice the fundamental (2128.40–2585.90 Hz) and appears to be a second harmonic. The dominant frequency has an upward frequency sweep toward the end of the call.

Forest Call II (Fig. 3).—This call is the longest of the sympatric call types, with an average duration of 281.35 ms, issued at a low calling rate (15–31 calls/min). It is also the most conspicuously pulsed call type to the human ear because individual pulses are temporally better defined by rising from and decaying back to background noise levels before another pulse is emitted. This is the only call type where pulse duty cycle (pulse duration/pulse period) is roughly 0.5. Call onset is gradual, reaching a peak and sustaining a plateau around mid-call. The number of pulses per call ranges from 10–17. The dominant frequency (4057.90–4953 Hz) is approximately twice the fundamental frequency (2028.90–2466.5 Hz) and is, thus, apparently the second harmonic, rising steadily during the call.

Forest Call III (Fig. 4).—This call is a comparatively short signal (average length 48.61 ms), issued at a marginally higher calling rate (48–60 calls/min). Unlike the other two calls, it is not pulsed. Call rise time is short, reaching the point of highest amplitude shortly after call onset. Both fundamental (2208–2679.5 Hz) and dominant (4654.6–5338.8 Hz) frequencies can be slightly higher than in the previous two forest call types. As in the previous call types, frequency rises during the call.

Adenomera hylaedactyla (Fig. 5).—Like Forest Call III, this is a short signal (average duration 46.02 ms). It is distinctly different from the other three calls at Tambopata in that

TABLE 2.—Means and ranges for morphometric measurements for all four Tambopata call types and toe tip shapes. All measurements expressed in mm.

Call type	Forest type I	Forest type II	Forest type III	<i>Adenomera hylaedactyla</i>
<i>n</i>	6	5	4	5
SVL	21.64	20.76	20.24	23.48
Head width	21.17–22.34	19.53–21.75	19.83–20.90	22.23–24.27
Head length	8.19	7.71	7.76	8.61
Eye/nostril distance	7.68–8.72	7.52–7.92	7.60–7.84	8.32–8.96
Thigh length	7.71	7.46	7.28	8.11
Shank length	7.52–8.00	7.28–7.60	7.12–7.44	7.92–8.48
Tarsus length	1.6	1.54	1.46	1.65
Foot length	1.52–1.68	1.36–1.60	1.44–1.50	1.60–1.68
Eye diameter	9.75	9.36	9.47	10.11
Tympanum diameter	8.97–10.43	9.13–9.62	9.37–9.62	9.62–10.76
Forearm length	10.51	9.75	9.63	10.92
Hand length	10.27–10.60	9.29–10.11	9.45–10.11	10.43–11.57
Toe tips	5.28	5.06	5.19	5.87
	4.80–5.68	4.96–5.20	4.80–5.63	5.36–6.40
	10.68	10.6	9.81	12.05
	9.62–11.25	9.94–11.08	9.50–10.02	11.49–13.04
	2.32	2.26	2.29	2.58
	2.16–2.48	2.16–2.32	2.19–2.32	2.40–2.80
	1.37	1.23	1.25	1.36
	1.20–1.52	1.12–1.44	1.12–1.36	1.28–1.52
	3.92	3.46	4.10	4.35
	3.04–4.48	3.20–4.00	3.92–4.38	4.00–4.80
	4.8	4.58	4.26	5.33
	4.40–5.20	4.08–4.88	4.16–4.40	4.88–6.08
	Slightly expanded to expanded	Slightly expanded to expanded	Expanded	Not expanded to slightly expanded

it has a much higher calling rate. Call rise time is short, and the signal has 4–6 pulses per call. Both fundamental and dominant frequencies are marginally lower than in any of the other sympatric call types. The dominant frequency rises sharply within each pulse.

Call Parameters and Morphological Features

A number of subtle differences have been identified as potentially useful, if used in combination, in separating the four sympatric morphs. The dorsal pattern has been considered a poor discriminating character (de la Riva, 1996), given its high intra- and interspecific variability. However, at least in the Tambopata populations, we found that subtle differences do exist, and they could potentially be used to identify the specific call types. Figure 6A–D depicts dorsal patterns of callers and their respective call types. *Adenomera hylaedactyla* and individuals making Forest Call I, observed in the field and in preserved condition, seem to present a greater intrapopulation variation in dorsal pattern than do the other call types, although this may be more related to sampling bias than to a lack of

variation in the other types; Forest Call I and *A. hylaedactyla* were the most frequently heard and encountered in the field. However, pattern variants in these call types do not overlap with dorsal patterns of the other two call types.

Forest Call II dorsal patterns (Fig. 6B) have symmetrical melanophore markings on the right and left sides. A clear, pale cream circular to oval marking is present in the scapular region, and, together with melanophores, it resembles the letter W (Fig. 6B). Individuals of Forest Call II have not been observed to have dorsal stripes.

Forest Call III (Fig. 6C) is generally the darkest of all *Adenomera* examined, with a dark, broad, discontinuous mid-dorsal stripe extending from the occiput of head to the waist. The stripe is discontinuous from the pectoral girdle to about half of the body length. Very discontinuous melanophores tend to parallel this stripe.

Adenomera hylaedactyla (Fig. 6D) is the most conspicuously marked of the the morphs at Tambopata, with a cream, mid-dorsal stripe from the occiput almost to the cloaca. In the scapular region, this stripe broadens and then

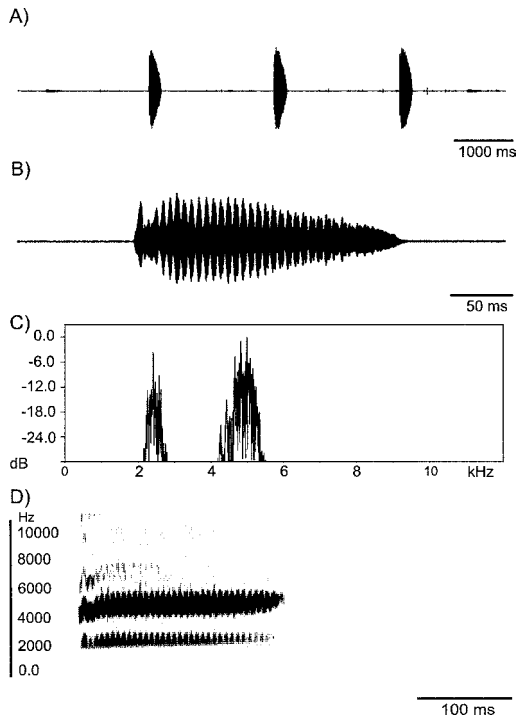


FIG. 2.—Forest Call I: A) oscillogram depicting calling pattern, B) waveform of one advertisement call at higher resolution, C) power spectrum, and D) spectrogram of one advertisement call.

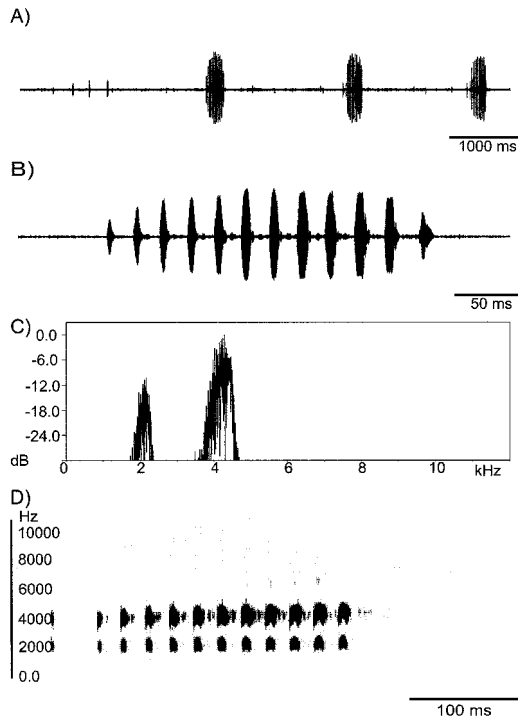


FIG. 3.—Forest Call II: A) oscillogram depicting calling pattern, B) waveform of one advertisement call at higher resolution, C) power spectrum, and D) spectrogram of one advertisement call.

narrows again to end in an oval marking similar to that of Forest Call II. Generally, about four, dark, continuous or discontinuous paravertebral or dorsolateral stripes are present. This morph usually has a fine, hairline stripe, from snout to cloaca, which can be distinguished from the broader mid-dorsal stripe by its different color.

A second feature that aids in distinguishing the four call type morphs is the nature of the supratympanic melanophores. However, this character is more variable than the dorsal pattern, and there are intermediate states among the different call types. This marking extends from the posterior margin of the eye and dorsal edge of the tympanum to the level of the insertion of the arm, following the outline of the supratympanic fold in specimens of Forest Call I and III and *A. hylaedactyla*. However, in Forest Call II, this broad marking tends to extend only to the posterior edge of the tympanum or halfway to the level of the insertion of the arm. In some individuals, some mottling is

present between the marking and the level of the arm. All *Adenomera* have a mark in the shape of an inverted triangle in the occipital region, but this triangle is more pronounced in Forest Call III than in *A. hylaedactyla*.

Toe tips are a third aid in the discrimination of *A. hylaedactyla* from the forest call types. All three forest call types possess toe tips that are slightly to fully expanded, whereas *A. hylaedactyla* has slender toes that are not expanded to slightly expanded (see Fig. 7). Forest Call III has the greatest expansion of toe tips.

A fourth feature that can be used in conjunction with the others mentioned previously is shapes of the snout and overall head. Although the difference is small, Forest Call III has the shortest snout of all four sympatric call types, while *A. hylaedactyla* and Forest Call I have a marginally longer snout. Forest Call II has a head shape that appears to be more subovoid or elongate than the other sympatric types.

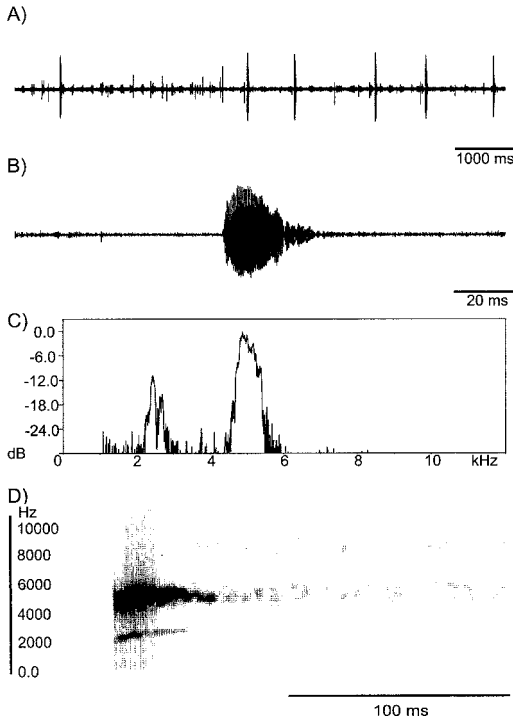


FIG. 4.—Forest Call III: A) oscillogram depicting calling pattern, B) waveform of one advertisement call at higher resolution, C) power spectrum, and D) spectrogram of one advertisement call.

Figure 8 depicts a three-dimensional scatterplot of pulses per call, dominant frequency, and call rate that separates the different call types. These parameters were chosen because of their general importance in species recognition in frogs. Two individuals of *A. hylaedactyla* were not included in this figure as pulses were not readily observable because of signal degradation. Although variation occurs within each call type, individual call types tend to cluster, and there is no observable overlap of data points for any one particular call. Calls of *A. hylaedactyla* are clustered separately from the three forest call types because of their higher call rate; all three forest call types aggregate closely together in this respect.

Table 3 gives results from a PCA for seven call variables for three species with pulsed calls. Principal component (PC) I accounts for just over half of the total variance. Call length and call rise time have the strongest negative loadings on PC I, suggesting that perhaps there is an inverse relationship between these tem-

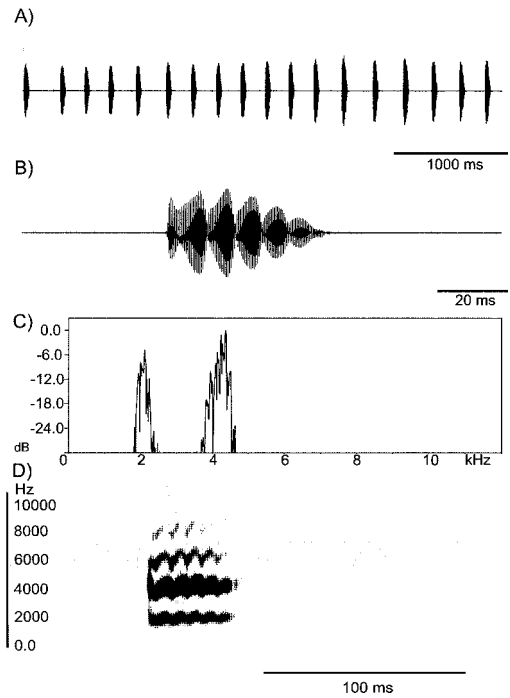


FIG. 5.—Advertisement call of *Adenomera hylaedactyla*: A) oscillogram showing calling pattern, B) waveform of one advertisement call at higher resolution, C) power spectrum, and D) spectrogram of one advertisement call.

poral parameters and factor I. Dominant frequency has a strong positive loading on PC II, but frequency modulation has a positive loading on PC I. It is not clear which PC accounts best for frequency-related parameters. Figure 9 depicts PCA for canonical variables 1 and 2 for advertisement call data for species with pulsed calls. There is no data overlap between the different categories. The separation between call types is very apparent, and all individuals within the same call type cluster together, suggesting that they indeed represent discrete groups.

Table 4 contains PCA loadings for 12 morphological variables for the four call types. Principal component I accounts for two-thirds of the variance in this data set and has generally strong loadings for all variables except arm length, suggesting that perhaps this component may represent overall variation in size. This variable, however, is the only one that has a strong positive loading on PC II.

Figure 10 is a plot of individual scores on PC I and II, based on a PCA of the morphometric

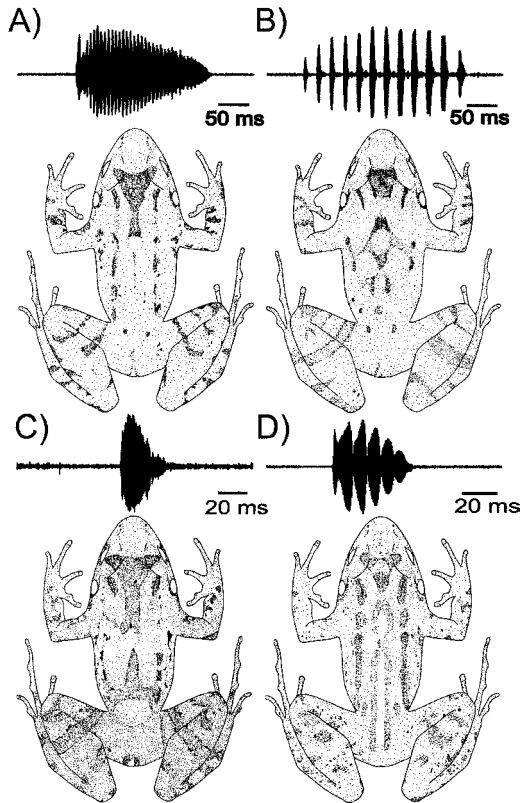


FIG. 6.—The four sympatric call types and the associated dorsal color patterns of the caller for each call type.

data for all call types. Contrary to the advertisement call data, the pattern in this case is not so clear, as there is considerable overlap and no significant separation between individuals from the four call types. However, there is some separation evident between Forest Call I and Forest Call III.

Table 5 summarizes the major features of the four sympatric call types in relation to each other.

DISCUSSION

This study shows that four distinct species of *Adenomera* occur at one site in southeastern Peru. The species differ markedly in features of their advertisement calls and, to a lesser extent, in their morphology and color pattern. It is not entirely clear which of these species, if any, correspond to the nominal *A. andreae* and *A. hylaedactyla*. Although the type locality for *A. andreae* is known (Peixeboi, Pará, northern Brazil [Müller, 1923]), no information is pro-

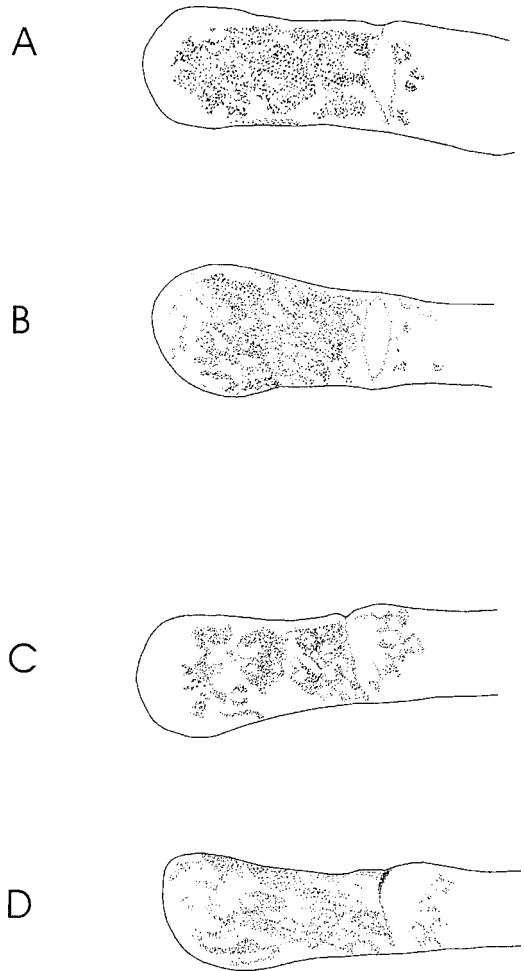


FIG. 7.—Shapes of tips of toes from frogs possessing each of the call types found in this study. From top to bottom: A) *Adenomera hylaedactyla*, B) Forest Call III, C) Forest Call II, and D) Forest Call I.

vided in the literature on vocalization or habitat. Both are critical in determining species identity in this case, since a call type morph can clearly exist in sympatry and syntopy with other morphs. In the case of *A. hylaedactyla*, the type locality is rather vague (“from the Napo or Upper Marañón” River, Peru [Cope, 1868]). Type material must be examined to determine the nominal species, which is not an easy task. In the holotype of *A. hylaedactyla* (ANSP 2240), the dorsal pattern is faded, rendering species identification difficult. Toe tips are expanded, though, as mentioned by Cope himself and subsequently confirmed by

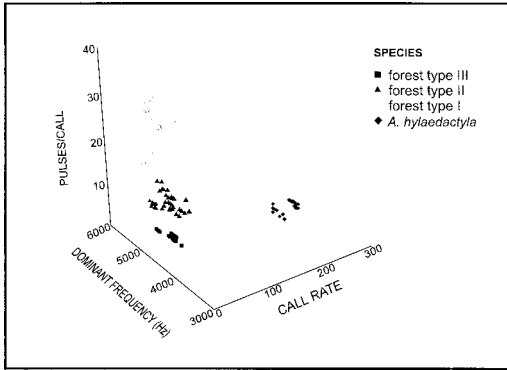


FIG. 8.—Scatterplot showing call-type clustering for pulses per call, dominant frequency, and call rate.

Heyer (1973). Four preserved specimens (ZSM 145/11/1–145/11/4) exist for *A. andreae*. The dorsal pattern of the lectotype (ZSM 145/11/4) is somewhat similar to that of Forest Call III, but much more uniform and less pigmented. However, each of the type specimens has a distinct dorsal pattern. Specimens ZSM 145/11/2 and ZSM 145/11/3 have patterns that are similar to some of those observed in individuals of Forest Call I from Tambopata; ZSM 145/11/1 resembles none of the dorsal patterns encountered at Tambopata. Because of the possibility that the type series could, in fact, consist of more than one species, determination of species identity based on this material alone is problematic.

The available literature on the advertisement calls of *Adenomera* is summarized in Table 6. Márquez et al. (1995) provided data on *A. diptyx* from Bolivia (although reported as *A. andreae*, the calls in this paper are of *A. diptyx* [I. de la Riva, personal communication]). The call type from Tambopata that most closely resembles that of *A. andreae* (Zimmerman and Bogart, 1984) is Forest Call III. However, these calls are shorter than those of *A. andreae* and, more importantly, have a higher fundamental frequency (up to 500 Hz difference) and dominant frequency. This variation suggests that Forest Call III may not represent the same species as that described by Zimmerman and Bogart (1984). The call of *A. diptyx* (Márquez et al., 1995) is similar to that of our *A. hylaedactyla*, although the populations at Tambopata have a higher calling rate than *A. diptyx* and differ in fine temporal features. The calls of *A. hylaedactyla*

TABLE 3.—Principal component loadings for seven call variables for three species with pulsed calls.

Variable	PC I	PC II
Call length	−0.936	0.175
Call rate	0.784	−0.572
Call rise time	−0.905	−0.338
Dominant frequency	−0.259	0.829
Frequency modulation	0.764	0.535
Pulse rate	0.694	0.696
Pulse rise time	0.494	−0.751
Proportion of variance explained	52.66	35.63
Cumulative variance explained	52.66	88.29

were reported by Heyer (1973), Márquez et al. (1995), Schneider et al. (1988), Schlüter (1980), and Straughan and Heyer (1976). The call parameters of our *A. hylaedactyla* generally agree with those of Márquez et al. (1995), except in the case of call rate that is somewhat higher at Tambopata; and, with regards to the presence of a pulsed component, the Tambopata calls were pulsed. The results of Márquez et al. (1995) seem to indicate a lack of pulses in the calls of *A. diptyx* and *A. hylaedactyla*. However, one of us (S. Reichle), has reviewed the original recordings of Márquez et al. (1995) for *A. hylaedactyla* and found that they are pulsed, as are those of *A. diptyx*. Pulses may be confused with strong amplitude modulation in noisy signals, as signals degrade and attenuate with increased distance between sender and receiver. Also, there is general agreement between our data and those of Schneider et al. (1988) for the shared presence of a third harmonic band and calls with pulsed components.

Calls figured in Heyer (1973) and later discussed in Straughan and Heyer (1976) originated from three localities in Brazil. Differences between two of these calls led Straughan and Heyer (1976) to suggest that the degree of difference of *A. hylaedactyla* was on a par with species differences in other genera of frogs. Calls from Tambopata differ from all of those discussed in Straughan and Heyer (1976) in call length; those from Tambopata are considerably shorter, in some cases being half the duration of the Brazilian calls. Moreover, call rates at Tambopata are higher than those from Jataí, Goiás, and Santo Antonio de Leverger, Mato Grosso, Brazil. Furthermore, calls at Tambopata lack an apparent fundamental frequency of 500 Hz,

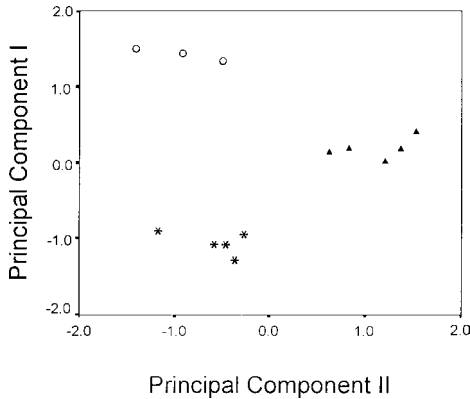


FIG. 9.—Graphic representation of individual scores on principal components I and II, based on a principal components analysis performed on call data for the three call types with pulsed components. Note that Forest Call III is not included as it is qualitatively different in this temporal parameter. Call types are represented by the following symbols: \circ = *Adenomera hylaedactyla*, * = Forest Call II, and \blacktriangle = Forest Call I.

whereas all three Brazilian recordings seem to possess this frequency band (although this could be an artifact of background noise). Schlüter's (1980) data from Panguana, Peru, seem to agree overall with ours, with the exception of a lower call rate compared to Tambopata and a call that is slightly longer than at Tambopata. Calling rate in many frogs can vary with social context and motivation. We also included results reported for populations in southeastern Brazil for comparative purposes (see Table 6), although it is very unlikely that any of the species in question would have such widespread distribution; this summary may prove useful for further work with this group. In short, the species we have called *A. hylaedactyla* and Forest Call III may correspond with literature descriptions from other localities, but Forest Calls I and II do not seem comparable to any previously reported advertisement signals in *Adenomera*.

Call Types and Habitat Associations

Heyer (1977) suggested that *A. andreae* and *A. hylaedactyla* are ecologically segregated: *A. andreae* is a diurnal forest floor species and *A. hylaedactyla* is a nocturnal open-formation species. We have noted ecological segregation and habitat associations among the call types at Tambopata. All four call types occur sympatrically. However, Forest Calls I and II were

TABLE 4.—Principal component loadings for 12 morphological variables for four sympatric call types of *Adenomera*.

Variable	PC I	PC II
SVL	0.947	-0.107
Head width	0.939	0.098
Head length	0.937	0.003
Eye-nostril	0.739	0.009
Thigh length	0.828	0.150
Shank length	0.910	-0.009
Tarsus length	0.711	0.467
Foot length	0.891	-0.265
Eye diameter	0.824	-0.085
Tympanum diameter	0.507	-0.452
Arm length	0.385	0.877
Hand length	0.917	-0.266
Proportion of variance explained	66.17	11.45
Cumulative variance explained	66.17	77.63

only heard and recorded in primary and secondary forests, particularly in areas with poorly drained soils that are easily flooded ("wet" forest habitat). Flooding is seasonal, and vegetation below 1 m is relatively dense compared to the other habitats. *Heliconia* plants are often found in this type of forest. Both call types are syntopic and synchronic; calling activity was recorded in late afternoons, often continuing into the night and resuming again at the break of dawn (the latter case for Forest Call I), and males of both call types were recorded within 1 m of each other. Forest Call III was only heard in the upland forest, in areas with sandy soils and generally good drainage. This type of forest is generally more open than the forests where Forest Calls I and II are heard, and palm trees appear to be more abundant in this environment ("high dry forest" habitat). This call was recorded in late afternoons, near dusk. The call of *A. hylaedactyla* was heard and recorded in clearings, mostly in disturbed areas immediately adjacent to rural lodges or near human habitations in rural townships. *Adenomera hylaedactyla* also call from within tall grass, tufts of grass near river banks and rural roads, underneath leaf litter below planted trees, and under or near rural buildings ("clearing" habitat). The call was heard and recorded mainly at dawn and dusk, although males also called well into the night. All males of all call types (except Forest Call III, for lack of evidence) call immediately after a downpour, irrespective of time of day.

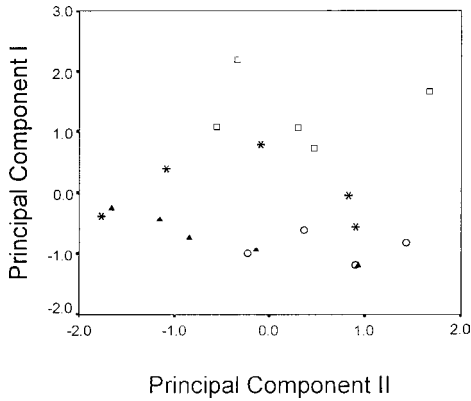


FIG. 10.—Graphic representation of individual scores on principal components I and II, based on a principal components analysis performed on morphometric data for all four sympatric species of *Adenomera*. Call types are represented by the following symbols: \circ = *Adenomera hylaedactyla*, \square = Forest Call III, * = Forest Call II, and \blacktriangle = Forest Call I.

Taxonomic Implications

Advertisement calls are important indicators of species identity since they often contribute to premating isolation among sympatric species (Duellman and Pyles, 1983). Because of their species specificity, it is possible to identify frogs on the basis of their vocalizations; it is even possible to discern hybrids, as they have calls that are intermediate of (Oliveira et al., 1991), or a mosaic of, parental types (Littlejohn et al., 1971 as quoted in Blair, 1974). When there are more acoustic signals than nominal species available, two questions have to be addressed. First, are these vocalizations truly indicative of specific status or are they the product of hybrids? Second, are they advertisement calls or part of an extended repertoire with different acoustic signals for different functions (e.g., agonistic calls, release calls, etc.)?

Regarding the first question, hybridization entails some type of range overlap in spatial distributions of parental species (in case of backcrossing fertile hybrids). In relation to the sympatric call types at Tambopata, only two are syntopic: Forest Calls I and II. If there are hybrids in this group, these two are the most likely candidates. However, hybrids indicate the presence of parental species, and if either of the two call types are the result of hybridization, another parental type should exist somewhere in the same environment. In addition, hybrid calls are either intermediate in nature or mosaics of the parental call types (Blair, 1974). None of the four call types seems to be intermediate of any other two.

If they are not hybrid calls, what is the likelihood that they may be different expressions of the same species that are issued in different behavioral contexts? Acoustic signals can be classified according to function (see Rand, 1988). Most vocalizations heard in the field are assumed, in the absence of contrary evidence, to be advertisement calls and have been treated as such in most of the existing literature. In the case of *Adenomera* at Tambopata, some shy or relatively unmotivated calling males were offered playbacks of their own call type in order to encourage them to continue calling until localization was achieved ($n = 8$ for call vouchers used in this analysis, $n = 2$ for Forest Call I, $n = 2$ for Forest Call II, $n = 3$ for *A. hylaedactyla*, and $n = 1$ for Forest Call III). All vouchered males changed their vocalizations to what was considered an aggressive or agonistic call; no individual male changed its call to any of the other call types reported here. This observation supports the notion that the different call types are not different signals in the repertoire of the same species but, rather, are bona fide advertisement calls. In addition, the subtle morpho-

TABLE 5.—Summary of call characteristics and habitat preferences for all four sympatric call types. Qualitative descriptions are based on calls in relation to each other.

Call type	Forest call I	Forest call II	Forest call III	<i>Adenomera hylaedactyla</i>
Call length	Long	Long	Short	Short
Call rate (calls/min)	Low	Low	Low	High
# pulses/call	20–39	10–17	1	4–6
Pulse rate	High	Low	—	High
Pulse duty cycle	1	0.5	1	1
Frequency sweeps within pulses	no	no	no	yes
Habitat	“Wet” forest	“Wet” forest	High dry forest	Clearing

TABLE 6.—Summary of acoustic parameters for *Adenomera* species derived from the published literature. Fo represents fundamental frequency.

Species	Temp (C)	Call length (ms)	Call repetition rate (calls/min)	Call interval	Fo (Hz)	Down freq (Hz)	Other freq (Hz)	Pulses	Source
<i>Adenomera andreae</i> Brazil, Amazonas	N/A	80 (60–100)	79.59/min (48.99–144.65)	960 (410–1660)	2210 (2190–2230)	4100–4430	?	?	Zimmerman and Bogart (1984)
<i>A. diptyx</i> (as <i>A. andreae</i>) Bolivia, Santa Cruz, Buenavista	N/A	66.5 (56.6–88.3)	82.5/min (52.6–128.4)	—	2228.6 (2180.8–2281.7)	4322.2 (4200–4502.9)	0	1	Márquez et al. (1995)
<i>A. hyllaedactyla</i> Bolivia, Santa Cruz, Puerto Almacén	N/A	56.8 (43.9–69.2)	132.2/min (117.8–149.6)	—	2240.2 (2079.8–2463.5)	4448.2 (4200–4785.6)	0	1	Márquez et al. (1995)
<i>A. hyllaedactyla</i> Brazil, Amazonas	23.9 & 23.8	59.87 & 73.11	—	350.15 & 390.26	<2000 (1800–1900)	3200–4000	5000–6000	7–10	Schneider et al. (1988)
<i>A. hyllaedactyla</i> Brazil									Heyer (1973); Straughan and Heyer (1976)
a) Goias, Jatai	a) 26	a) 130	a) 82/min	—	a) <500; 1860–2600	a) 3700–4833	a) 5966–6600; 8000		
b) Mato Grosso, Sto. Antonio de Leverger	b) 29	b) 110	b) 82/min	—	b) <500	b) 3833–5133	b) 5925–7300; 8000		
c) Mato Grosso, Chapada dos Guimarães	c) 19	c) 80	c) 190/min	—	c) <500; 2000–3270	c) 4240–5380	c) 6375–7725		
<i>A. hyllaedactyla</i> Peru, Panguana	26	80	150/min	—	1700–2200 1800–2300	3500–4500 3400–4500	0		Schlitter (1980)
<i>A. marmorata</i> Brazil, São Paulo, Paranaipacaba	20	100	75/min	—	2200	5200	0		Barrio (1965)
<i>A. marmorata</i> Brazil, Rio de Janeiro, Tijuca	22	100	94/min	—	broad Fo <1000	4500–5600			Straughan and Heyer (1976); figure in Heyer (1973)
<i>A. marmorata</i> Brazil, São Paulo, Boracéia	18	40–70	0.8–1.4/s= 48–84/min	—	None	4500–5400 (=Fo)	0	1	Heyer et al. (1990); figure in Heyer (1973)

logical differences associated with each call type provide evidence against the call repertoire hypothesis.

From our results, it is clear that the acoustic diversity is greater than named taxonomic diversity of *Adenomera* in the Amazon Basin. Recordings from elsewhere in the Basin also seem to support this inference (Angulo and Icochea, 2003; A. Angulo and J. Reichle, unpublished data; Boistel et al., 2003). This evidence indicates that *Adenomera* contains many more than the currently recognized species and that the use of acoustic signals as an initial means in untangling species identity in this group will be useful. We conclude that the four different call types that occur sympatrically in the TNR represent four different species. In order to avoid further confusion until we can clarify the identities of the nominal *Adenomera*, we refrain from describing the (at least) two new species. However, it is possible that none of the species at Tambopata are conspecific with *A. andreae* and all three forest species may be undescribed. Or, it may also be possible that any of the Tambopata *Adenomera* may be one of the synonyms that were later brought under *A. andreae* or *A. hylaedactyla* (see Heyer, 1973). Ongoing research into morphological correlates and molecular and behavioral aspects may shed more light on the identities of these frogs and their relationships to each other.

RESÚMEN

El género *Adenomera* se ha caracterizado por ser un difícil grupo para estudios de sistemática dada la semejanza general y la variación poblacional entre las especies miembros del género. Fueron reportadas dos especies para la región Amazónica Peruana: *Adenomera andreae* y *Adenomera hylaedactyla*. Sin embargo, grabaciones acústicas provenientes de la Reserva Nacional de Tambopata, en el sureste Peruano, revelaron que existen cuatro diferentes tipos de cantos en simpatria y que son muy distintivos en términos de sus parámetros acústicos y al oído humano. También parecen haber ciertas diferencias morfológicas sutiles, aunque estas son, en líneas generales, especies crípticas. Concluimos que existen por lo menos cuatro especies simpátricas en Tambopata y que *Adenomera* tiene una mayor diversidad específica de lo que actualmente se le reconoce.

Acknowledgments.—We thank the Instituto Nacional de Recursos Naturales (INRENA), Peru, for granting appropriate permits; Explorer's Inn, Newton College's Sachavacayoc Centre; P. V. Ipenburg and D. Bruggers, Tambopata Research Centre—Rainforest Expeditions; and K. Holle for logistic support and access to their facilities and areas during field work. G. K. Morris reviewed the manuscript and provided helpful comments. We are grateful to W. R. Heyer and R. McDiarmid, Smithsonian Institution, for helpful comments and enabling loans of acoustic archives and specimens. Thanks to F. Glaw, Zoologische Staatssammlung Munchen, and N. Gilmore, Academy of Natural Sciences of Philadelphia, for loan of type specimens. We thank I. de la Riva and R. Márquez for providing recordings of *Adenomera diptyx*. Field research support for A. Angulo was provided by operating NSERC grant #4946 to G. K. Morris. Special thanks go to M. Matthews and to V. Morales for help in the field.

LITERATURE CITED

- ALMEIDA, A. P., AND A. ANGULO. 2002. *Adenomera aff. marmorata* (NCN). Reproduction. *Herpetological Review* 33:197–198.
- ANGULO, A., AND J. ICOCHEA. 2003. *Adenomera cf. andreae* (NCN). Vocalization. *Herpetological Review* 34:47–48.
- BARRIO, A. 1965. Afinidades del canto nupcial de las especies cavícolas del género *Leptodactylus* (Anura—Leptodactylidae). *Physis* 25:401–410.
- BLAIR, W. F. 1974. Character displacement in frogs. *American Zoologist* 14:1119–1125.
- BOISTEL, R., J.-C. DE MASSARY, AND A. ANGULO. 2003. Description of a new species of the genus *Adenomera* (Amphibia, Anura, Leptodactylidae) from French Guiana. *Amphibia-Reptilia*: In press.
- BOKERMANN, W. C. A. 1956. Sobre una nueva especie de *Leptodactylus* del Brasil (Amphibia). *Neotropica* 2:37–40.
- COCROFT, R. B., AND M. J. RYAN. 1995. Patterns of advertisement call evolution in toads and chorus frogs. *Animal Behaviour* 49:282–303.
- COPE, E. D. 1868. An examination of the Reptilia and Batrachia obtained by the Orton Expedition to Ecuador and the Upper Amazon, with notes on other species. *Proceedings of the Academy of Natural Sciences Philadelphia* 1868:96–140.
- DE LA RIVA, I. 1995. A new reproductive mode for the genus *Adenomera* (Amphibia: Anura: Leptodactylidae): taxonomic implications for certain Bolivian and Paraguayan populations. *Studies on Neotropical Fauna and the Environment* 30:15–29.
- . 1996. The specific name of *Adenomera* (Anura: Leptodactylidae) in the Paraguay River Basin. *Journal of Herpetology* 30:556–558.
- DUCELLMAN, W. E., AND R. A. PYLES. 1983. Acoustic resource partitioning in anuran communities. *Copeia* 1983: 639–649.
- FOUQUETTE, M. J., JR. 1960. Isolating mechanisms in three sympatric treefrogs in the Canal Zone. *Evolution* 14: 484–497.
- FROST, D. R. 2002. *Amphibian Species of the World: an online reference*. V2.21 (15 July 2002). <http://research.amnh.org/herpetology/amphibia/index.html>

- HEYER, W. R. 1973. Systematics of the marmoratus group of the frog genus *Leptodactylus* (Amphibia, Leptodactylidae). Contributions in Science of the Natural History Museum of the Los Angeles County 251:1–50.
- . 1974. Relationships of the *marmoratus* species group (Amphibia, Leptodactylidae) within the subfamily Leptodactylinae. Contributions in Science of the Natural History Museum of the Los Angeles County 253:1–46.
- . 1977. A discriminant function analysis of the frogs of the genus *Adenomera* (Amphibia:Leptodactylidae). Proceedings of the Biological Society of Washington 89:581–592.
- . 1984. The systematic status of *Adenomera griseigularis* Henle, with comments on systematic problems in the genus *Adenomera* (Amphibia: Leptodactylidae). Amphibia-Reptilia 5:97–100.
- HEYER, W. R., AND L. R. MAXSON. 1982. Distributions, relationships, and zoogeography of lowland frogs. The *Leptodactylus* complex in South America, with special reference to Amazonia. Pp. 375–388. In G. T. Prance (Ed.), Biological Diversification in the Tropics. Columbia University Press, New York, New York, U.S.A.
- HEYER, W. R., A. S. RAND, C. A. GONÇALVES DA CRUZ, O. L. PEIXOTO, AND C. E. NELSON. 1990. Frogs of Boracéia. Arquivos de Zoologia, São Paulo 31:231–410.
- HILL, R. A., AND G. M. FOODY. 1994. Separability of tropical rain-forest types in the Tambopata-Candamo Reserved Zone, Peru. International Journal of Remote Sensing 15:2687–2693.
- KELLER, E. 1994. Signalize™ Version 3.12. Infosignal Inc., Lausanne, Switzerland.
- KWET, A., AND A. ANGULO. 2002. A new species of *Adenomera* (Anura, Leptodactylidae) from the *Araucaria* forest of Rio Grande do Sul (Brazil), with comments on the systematic status of southern populations of the genus. Alytes 20:28–43.
- MÁRQUEZ, R., I. DE LA RIVA, AND J. BOSCH. 1995. Advertisement calls of Bolivian Leptodactylidae (Amphibia, Anura). Journal of Zoology, London 237:313–336.
- MÜLLER, L. 1923. Neue oder seltene Reptilien un Batrachier der Zoologischen Sammlung des bayr. Staates. Zoologischen Anzeiger 57:39–54.
- OLIVEIRA, M. E., M. PAILLETTE, H. D. ROSA, AND E. G. CRESPO. 1991. A natural hybrid between *Hyla arborea* and *Hyla meridionalis* detected by mating calls. Amphibia-Reptilia 12:15–20.
- RAND, A. S. 1985. Tradeoffs in the evolution of frog calls. Proceedings of the Indian Academy of Sciences (Animal Sciences) 94:623–637.
- . 1988. An overview of anuran acoustic communication. Pp. 415–431. In B. Frittsch, M. J. Ryan, W. Wilczynski, T. E. Hetherington, and W. Walkowiak (Eds.), The Evolution of the Amphibian Auditory System. John Wiley & Sons, New York, New York, U.S.A.
- RYAN, M. J. 1983. Sexual selection and communication in a neotropical frog, *Physalaemus pustulosus*. Evolution 37:261–272.
- SCHLÜTER, A. 1980. Bio-akustische untersuchungen an leptodactyliden in einem begrenzten gebiet des tropischen regenwaldes von Peru. Salamandra 16:227–247.
- SCHNEIDER, H., G. JOERMANN, AND W. HÖDL. 1988. Calling and antiphonal calling in four neotropical anuran species of the family Leptodactylidae. Zoologische Jahrbücher Abteilung für Allgemeine Zoologie und Physiologie der Tiere 92:77–103.
- STRAUGHAN, I. R., AND W. R. HEYER. 1976. A functional analysis of the mating calls of the neotropical frog genera of the *Leptodactylus* complex (Amphibia, Leptodactylidae). Papéis Avulsos de Zoologia, São Paulo 29:221–245.
- ZIMMERMAN, B. L., AND J. P. BOGART. 1984. Vocalizations of primary forest frog species in the central Amazon. Acta Amazonica 14:473–519.

Accepted: 13 March 2003

Associate Editor: Joseph Mendelson III

APPENDIX I

All recordings listed here are from the Tambopata National Reserve and adjacent buffer zone, Departamento de Madre de Dios, Peru. Examined specimens (other than type material) are from different localities in the Departamento de Madre de Dios.

Recordings and Voucher Specimens Examined

Forest Call I: ROM 40110, recorded 6 January 1999 at 1720 h by A. Angulo, air temperature 24 C, Tape 1; ROM 40111, recorded 6 February 1999 at 2116 h by A. Angulo, air temperature 25 C, Tape 4; ROM 40321, recorded 9 February 1999 at 2143 h by A. Angulo, air temperature 26 C, Tape 4; USNM 342984, recorded 30 December 1988 at 0045 h by R. B. Cocroft, air temperature 22.3 C, USNM Tape 203, cut 8; USNM 342983, recorded 30 December 1988 at 0007 h by R. B. Cocroft, air temperature 22.2 C, USNM Tape 203, cut 6

Forest Call II: USNM 342978, recorded 29 December 1988 at 2315 h by R. B. Cocroft, 22.2 C, USNM Tape 203, cut 3; USNM 342979, recorded 29 December 1988 at 2359 h by R. B. Cocroft, air temperature 22.2 C, USNM Tape 203, cut 5; USNM 342980, recorded 30 December 1988 at 0030 h by R. B. Cocroft, air temperature 22 C, USNM Tape 203, cut 7; USNM 342981, recorded 31 December 1988 at 0030 h by R. B. Cocroft, air temperature 23.2 C, USNM Tape 203, cut 13; USNM 343231, recorded 19 November 1990 at 2300 h by R. B. Cocroft, air temperature 22.6 C, Tape 267, cut 12

Forest Call III: USNM 343236, recorded 3 November 1990 at 1655 h by R. B. Cocroft, air temperature 16.6 C, USNM Tape 265, cut 2; USNM 343232, recorded 2 November 1990 at 1715 h by R. B. Cocroft, air temperature 26.2 C, USNM Tape 265, cut 3; USNM 343237, recorded 3 November 1990 at 1820 h by R. B. Cocroft, air temperature 25.9 C, USNM Tape 265, cut 5

Adenomera hylaedactyla: ROM 40105, recorded 26 January 1999 at 1911 h by A. Angulo, air temperature 25.5 C, Tape 3; ROM 40106, recorded 29 January 1999 at 1904 h by A. Angulo, air temperature 25 C, Tape 3; ROM 40109, recorded 29 March 1999 at 0103 h by

A. Angulo, air temperature 27 C; USNM 342986, recorded 6 January 1989 at 1830 h by R. B. Cocroft, air temperature 24.2 C, USNM Tape 206, cut 1; USNM 342985, recorded 30 December 1988 at 1845 h by R. B. Cocroft, air temperature 25 C, USNM Tape 203, cut 10

Additional Specimens Examined

Adenomera andreae type series: ZSM 145/1911/1-4 (four specimens)

Adenomera hylaedactyla: holotype ANSP 2240

Other Tambopata Specimens Examined

Forest Call I: USNM 268933–34, 268936, 247295, 247290, 242629; ROM 40110–17, 40321–26; MHNSM 18030, 18042

Forest Call II: USNM 268932, 268935, 268937–38, 247291–94, 247625–28

Forest Call III: USNM 343235

Adenomera hylaedactyla: USNM 342985–86, 345269 (Pakitza), 345270 (Pakitza); ROM 40102–04, 40107–08, 40327–28, 40330; MHNSM 18031, 18048

Herpetologica, 59(4), 2003, 504–512

© 2003 by The Herpetologists' League, Inc.

A NEW SPECIES OF *STEFANIA*
(ANURA: HYLIDAE: HEMIPHRACTINAE) FROM THE SUMMIT OF
CERRO AUTANA, ESTADO AMAZONAS, VENEZUELA

CÉSAR LUIS BARRIO-AMORÓS^{1,3} AND OSWALDO FUENTES²

¹Fundación Andígena. Apartado postal 210. 5101-A, Mérida, Venezuela

²Colección de Herpetología, Museo de Biología, Universidad Central de Venezuela, Caracas, Venezuela

ABSTRACT: We describe a new species of *Stefania* from the summit of Cerro Autana in Amazonas, Venezuela. It is the westernmost species hitherto known for the genus, being 200 km northwest of Cerro Huachamacari, the nearest known locality for any other *Stefania*. The new species is distinguished from other species of *Stefania* by the following combination of characters: fronto-parietal ridges present but reduced, foot webbing basal, discs on fingers and toes small, post-tympanic warts absent, and head as long as wide. Based on these traits, the species can be placed in the *Stefania evansi* group of Rivero.

Key words: Amphibia; Anura; Biogeography; Cerro Autana; Estado Amazonas; Hemiphractinae; Hylidae; New species; Venezuela

IN VENEZUELA, Hemiphractine frogs are represented by 4 genera (*Cryptobatrachus*, *Flectonotus*, *Gastrotheca*, and *Stefania*) and 21 species (1, 2, 6, and 12, respectively) (Barrio-Amorós, 1998; Frost, 2000; unpublished data for *Cryptobatrachus*). Among these, the genus *Stefania* has undergone many systematic changes. Since Rivero (1968) separated *Stefania* from *Cryptobatrachus*, the number of species has increased dramatically. The discovery of new species has coincided with the progressive exploration of the Guiana Shield, one of the most inaccessible and unknown areas in the world.

Boulenger's (1904) *Hyla evansi* was first considered to be a *Cryptobatrachus* by Ruthven (1922). Rivero (1961) described *H. marahuaquensis* and later he (Rivero, 1968) separated *C. evansi* from the Colombian species of *Cryptobatrachus* and erected the genus *Stefania* for *C. evansi*, tentatively placing *H. marahuaquensis*, as well as three new species (*S. ginesi*, *S. goini*, and *S. woodleyi*), in the new genus. Later, Rivero (1970) described an additional species (*S. scalae*) and assigned the six known species of *Stefania* to two well defined species groups, the *S. evansi* group (lowland to mid-elevation species with heads longer than wide: *S. evansi*, *S. marahuaquensis*, *S. scalae*, and *S. woodleyi*) and the *S. goini* group (high elevation inhabitants with heads wider than long: *S. ginesi* and *S. goini*).

³ CORRESPONDENCE: e-mail, cesarlba@yahoo.com

Duellman and Hoogmoed (1984) described two species (*S. riae* and *S. roraimae*) and synonymized *S. scalae* with *S. evansi*. The latest revision of Venezuelan *Stefania* (Señaris et al., 1996) contained descriptions of five additional new species (*S. oculosa*, *S. percristata*, *S. riveroi*, *S. satelles*, and *S. schuberti*), resurrected *S. scalae* from synonymy with *S. evansi*, and noted the probability of more undescribed taxa. The suggestion was proven to be true by the discovery of *S. tamacuarina* by Myers and Donnelly (1997). MacCulloch and Lathrop (2002) recently named three new species from Guyana.

During the first expedition to the summit of Cerro Autana, an isolated tepui 85 km south of Puerto Ayacucho in 1971, another unknown *Stefania* was collected by the team of the Venezuelan explorer Charles Brewer-Carías. We describe the species herein.

MATERIALS AND METHODS

Measurements were taken with a caliper (to 0.1 mm) and are expressed in millimeters (mm). Morphological terms and measurements are those of Duellman and Hoogmoed (1984) and Myers and Donnelly (1997). The webbing formula follows Myers and Duellman (1982). Measurements considered are: snout-vent length (SVL); tibia length (TL); femur length (FeL); foot length (FL); hand length (HL); head width (HW); head length (HeL); internarial distance (InD); upper eyelid width (UEW); interorbital distance (IOD); eye to posterior edge of nostril (EN); eye diameter (ED); tympanum diameter (TD); 3 finger disc width (FD); 4 toe disc width 4TD; depth of the head (DeH); distance between the anterior edge of the eye to the tip of snout (ETS); eye tympanum distance (ETD); 1 finger length (1FiL); 2 finger length (2FiL). Acronyms are AMNH (American Museum of Natural History, New York, USA), CVULA (Colección de Vertebrados, Universidad de los Andes, Mérida, Venezuela), EBRG (Museo de la Estación Biológica de Rancho Grande, Maracay, Venezuela), FMNH (Field Museum of Natural History, Chicago, USA), MBUCV (Museo de Biología de la Universidad Central de Venezuela, Caracas, Venezuela), MHNLS (Museo de Historia Natural La Salle, Caracas, Venezuela), OUM (Oxford University Museum, Oxford, UK). Cranial drawings are based on

X-ray transparencies. Comparative data of other species were taken from Duellman and Hoogmoed (1984), MacCulloch and Lathrop (2002), Myers and Donnelly (1997), Rivero (1961, 1968, 1970), and Señaris et al. (1996).

Stefania breweri sp. nov.

Holotype.—MBUCV 6574, an unsexed specimen from the summit of Cerro Autana (Wahari Kuaway), near the north ridge (4° 52' N, 67° 27' W), 1250 m elevation, Municipio Atures, Estado Amazonas, Venezuela; collected 12 February 1971, by Carlos J. Naranjo.

Diagnosis.—A medium sized or possibly large *Stefania* (the only known specimen is 49.6 mm SVL); head as long as wide; frontoparietal ridges conspicuous; canthus rostralis distinct, angular, straight; tympanum somewhat less than 3/4 diameter of eye. First finger distinctly longer than second; discs on fingers and toes very small; toes webbed basally; hind limbs very long. Skin on dorsum smooth, with striking pattern of dorsolateral stripes and a discrete pale white interorbital bar; limbs with transverse brown bars on a pale ground color; venter pinkish, slightly transparent. *Stefania breweri* is a member of the *S. evansi* group (Rivero, 1970) and can be distinguished from other species of that group by the following combination of characters (those of *S. breweri* in parentheses). *Stefania scalae* has extensive toe webbing (basal), medium sized discs on fingers and toes (very small), no frontoparietal ridges (present). *Stefania evansi* has extensive webbing on the foot (basal), supernumerary tubercles on hands indistinct or absent (few but distinct). *Stefania riae* has knobs on the canthus rostralis (absent), no frontoparietal ridges (present), large oval discs on outer fingers (very small). *Stefania roraimae* has no frontoparietal ridges (present), enlarged discs on fingers (very small), supernumerary tubercles absent (present). *Stefania marahuaguensis* has post-tympanic cuneiform warts on the tympanic area and anterior part of the dorsum (absent), enlarged discs on fingers and toes (very small). *Stefania percristata* has prominent frontoparietal ridges (present but reduced), five teeth on vomers (three-four), frontoparietal bones fused but with two small fontanelles (without fontanelles), nasal bones narrow, not

TABLE 1.—Measurements (in mm) of *Stefania breweri* and other Venezuelan *Stefania* of similar size. Data on the other species are taken from Señaris et al. (1996) and Myers and Donnelly (1997).

Characters	<i>S. breweri</i>	<i>S. tamacuarina</i>	<i>S. ginesi</i>	<i>S. oculosa</i>	<i>S. satelles</i>
	MBUCV 6574	AMNH 131428	FMNH 74041	MHNS 12961	MHNS 10433
SVL	49.6	50	55	55.3	56.6
TL	32.5	30	33	33.1	29.5
FeL	29.1	—	29.5	33.8	32.2
FL	23.6	22.2	24.5	43.5	46.7
HL	14.3	15.9	—	—	—
HW	18.5	20	23	22.6	21.2
HeL	18.5	19.7	20	20.9	20.8
InD	3.0	3.5	—	—	—
UEW	5.0	5.0	—	—	—
IOD	5.5	5.5	—	5.5	5.1
EN	4.8	6.0	—	—	—
ED	6.7	6.5	—	8.8	6.6
TD	3.2	3.5	—	4.0	4.6
FD	1.7	2.9	—	—	—
4TD	1.2	2.4	—	—	—
DeH	8.7	—	—	—	—
ETS	6.6	—	—	7.2	5.0
ETD	2.0	—	—	—	—
1FiL	10	—	—	—	—
2FiL	7.2	—	—	—	—

in contact (broad, in contact). *Stefania tamacuarina* has knobs on the canthus rostralis (absent), enlarged discs on outer fingers and toes (small). *Stefania woodleyi* has granular to shagreened dorsal skin (smooth), frontoparietal ridges absent (present), supernumerary tubercles absent (small). *Stefania ackawaio* has shagreened dorsal skin (smooth), discs on hands and feet large (small), tubercles on upper eyelid (absent), dorsolateral stripes absent (present). *Stefania ayangannae* has supernumerary tubercles on hands and foot numerous, small, distinct (few), canthus rostralis curved (straight). Morphologically, *S. ayangannae* is the species that most closely resembles *S. breweri*. However, the known localities of these species are about 700 km apart, with all other species of *Stefania* occurring in between.

Six *Stefania* (*S. evansi*, *S. goini*, *S. marahuacensis*, *S. riae*, *S. roraimae*, and *S. scalae*) are known to have a similar color pattern of dorsolateral pale stripes. *Stefania tamacuarina* also has a somewhat similar pattern, with dark brown blotches on a lighter ground dorsal color, but without dorsolateral stripes. However, we cannot base a diagnosis upon such a variable feature as color pattern, es-

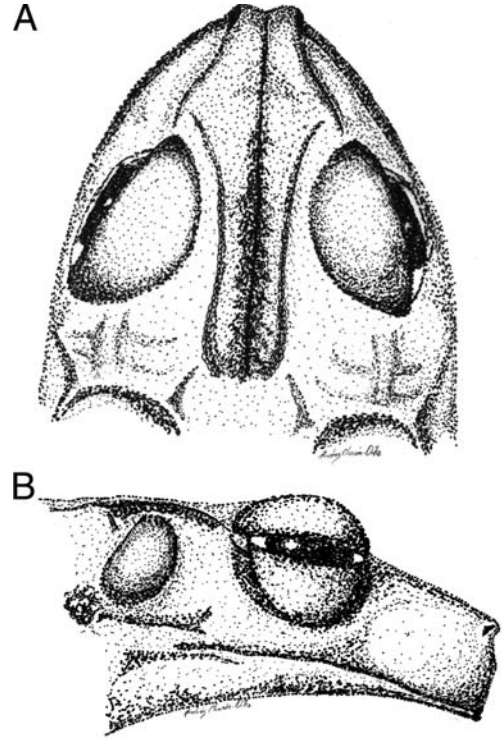


FIG. 1.—Dorsal (A) and lateral (B) view of the head of *Stefania breweri* sp. nov. (Holotype, MBUCV 6514). Scale = 10 mm.

pecially in *Stefania*. The other species of *Stefania* belong to the *goini* group, which is distinguishable from the new species by head proportions (wider than long; Table 1).

Description.—Head as wide as long, distinctly wider than adjacent part of body; depth of head slightly less than half length of head; snout subacuminate in dorsal view (Fig. 1A), truncate in profile (Fig. 1B), short, its length approximately equal to diameter of eye; canthus rostralis distinct, angular, straight, without knobs; loreal region strongly concave, sloping to lips; nostrils protuberant, directed laterally and slightly posterodorsally, immediately below canthus rostralis; distance between nostrils 55% of interorbital distance; interorbital region concave; interorbital space distinctly concave because of frontoparietal ridges, which continue to back of skull; temporal region sloping, not concave; tympanum distinct, large, ovoid, diameter equal to half of horizontal diameter of eye, surrounded by an ossified annulus, separated from eye by

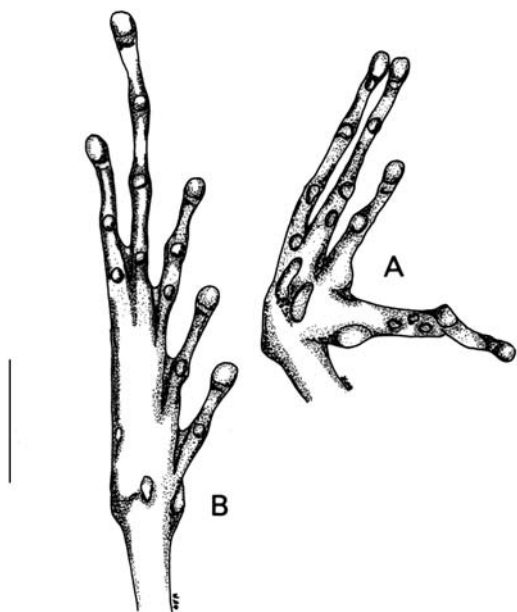


FIG. 2.—Ventral views of hand (A) and foot (B) of *Stefania breweri* sp. nov. (Holotype, MBUCV 6514). Scale = 5 mm.

a distance of half diameter of eye; supratympanic fold narrow, distinct, angular, extending from posterior corner of eye to above insertion of forelimb, obscuring upper edge of tympanum; choanae moderate in size, oval; dentigerous processes of vomers short, each bearing three and four teeth on vomerine processes, transverse between choanae; pupil horizontal; palpebral membrane pale, without dark edge or reticulations.

Skin on dorsum and head, upper eyelids, temporal and loreal regions, throat, and limbs smooth; skin on chin, throat and chest smooth, belly and flanks finely granular; cloacal opening directed posteriorly at upper level of thighs.

Thenar tubercle large, distinct, elongate, ovoid (Fig. 2A); palmar tubercle distinct, bifid; subarticular tubercles large, distinct, round; supernumerary tubercles on palm few, small, round. Relative finger length $II < I < IV < III$; first finger distinctly longer than second (72% of length of finger I); third and fourth fingers fused at base; fingers unwebbed; discs on fingers small, slightly wider than penultimate phalange, smaller on first two fingers, largest on outer ones; width of larger discs

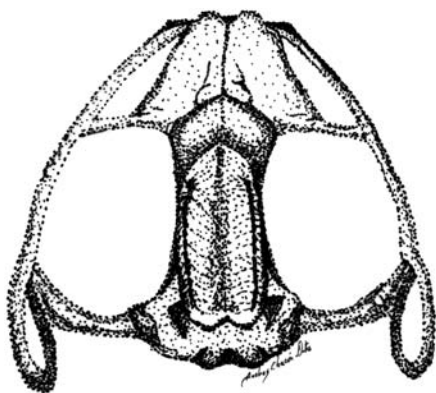


FIG. 3.—Dorsal view of the skull of *Stefania breweri* sp. nov. (Holotype, MBUCV 6514). Scale = 10 mm.

equal to 10% of length of diameter of tympanum.

Inner metatarsal tubercle relatively large, elongate (Fig. 2B); outer metatarsal tubercle smaller, indistinct. Subarticular tubercles large, distinct, single, round. Supernumerary tubercles distinct, small, round, present mainly on proximal segments. Relative lengths of adpressed toes $I < II < III < V < IV$; third toe slightly shorter than fifth; toes webbed basally; webbing formula $I \ 2 \frac{1}{3} - 2 \frac{1}{2}$ $II \ 2 - 3 \frac{1}{2}$ $III \ 2 \frac{1}{2} - 3 \ \frac{1}{3}$ $IV \ 3 \frac{1}{2} - 2$ V ; toe discs ovoid, small, wider than penultimate phalange, smaller than fingers discs; heels of adpressed limbs overlap considerably.

Data on color in life is not available. In preservative, the dorsum is pale orange, with a discrete pale white interorbital bar, connected on the upper eyelids with fine white dorsolateral stripes. In dorsal view, the loreal region appears to be as white as the interorbital bar; the upper eyelids blackish; four round dark brown spots present between the dorsolateral stripes in the middle and posterior part of the dorsum; flanks whitish with a few dark brown bars contacting the exterior edge of the dorsolateral stripes; dorsal surfaces of the thighs with diffuse dark brown bars on a paler background; shank and feet conspicuously paler than body; suborbital brown and white bars present; tympanum distinctly paler than surrounding area; throat, chest and belly uniformly pinkish, and somewhat transparent.

Cranial osteology.—Based on X-ray transparencies of the holotype (Fig. 3), the skull is

well ossified; nasals broad, in medial contact throughout their length, protruding anteriorly beyond premaxillae; sphenethmoid in contact with nasals and frontoparietals; frontoparietals bearing lateral crests throughout their length; crista parotica fused totally with frontoparietals and exoccipital; zygomatic ramus of squamosal in contact with maxilla; otic ramus of squamosal in contact with crista parotica; quadratojugal in contact with maxilla.

Habitat.—The summit of Cerro Autana (Fig. 4A,B) is dominated by an open swampy landscape with submesothermic herbaceous vegetation characteristic of intermediate elevations from 500–1500 m and temperatures of 18–24 C in the Guiana Shield (Huber and Alarcon, 1988). The dominant plant taxa are *Brocchinia hechtiioides* and *Kunhardtia rhodantha* (Steyermark, 1974). At the edges of the tepui, there are areas of exposed rock where several species of terrestrial orchids, plus *Navia pungens* and *Stegolepys pulchella* are dominant. On the northern part of the summit is a central dome that rises some 55 m above the grassland. Around this prominence, as well as along the crevices that channel water towards the northern and southern cliffs, is a humid environment supporting a dwarf forest of *Clusia* and many epiphytes. *Stefania breweri* was found within the tubular rolled leaves of a *Brocchinia* (Fig. 4B). Most species of *Stefania*, such as *S. evansi*, *S. goini*, *S. marahuacuensis*, *S. oculosa*, *S. percristata*, *S. scalae*, and *S. woodleyi*, are known to be rocky stream bank inhabitants (Duellman and Hoogmoed, 1984; Rivero, 1970; Señaris et al., 1996). *Stefania ginesi*, *S. satelles*, and *S. shuberti* are inhabitants of the high summits of tepuis from 1750–2600 m and have been found along creeks, but also under rocks, in bromeliads (*Brocchinia*), and on moss (Duellman and Hoogmoed, 1984; Gorzula and Señaris, 1998; Señaris et al., 1996). *Stefania riveroi* has been found on rocks at night (Señaris et al., 1996).



FIG. 4.—(Upper) panoramic view of Cerro Autana. (Lower) summit of Cerro Autana, showing typical congregations of terrestrial bromeliads (*Brocchinia hechtiioides*); white arrow indicates the place where *Stefania breweri* sp. nov. was found. Photos by Charles Brewer-Carias.

There is no literature about the ecology of *S. riae*, but Barrio-Amorós observed this species at Sarisariñama tepui in a sinkhole at 1000 m, with no flowing or standing water, only moist mossy walls and rocks with crevices and caves. *Stefania ayangannae*, *S. ackawaio*, and *S. coxi* were found away from water on branches of trees or woody shrubs, or on bromeliads, 1–5 m above the ground in a humid cloud forest at around 1500 m (MacCulloch and Lathrop, 2002). Because reproduction in *Stefania* is not dependent on free water, the presence of *S. breweri* on a tepui summit without constant water is not unusual. The only other frog species inhabiting the summit of Autana is *Leptodactylus lithonaetes*, which may use rain water for reproduction.

Distribution.—This species is known only from the type locality. The Cuao-Sipapo massif (Serranía de Paraque), of which Cerro Autana (Fig. 4A) seems to be a remnant, is nearby. *Stefania breweri* may occur on this massif as well.

Etymology.—The specific epithet is a patronym for Charles Brewer-Carías, to whom we are grateful for help and encouragement. Frank and Ramus (1995) proposed common names for *Stefania* species, without taking into account the peculiar distinctiveness of the genus, and named them simply “treefrogs,” when only a few species are known to frequent trees. We suggest the English common name of “Brewer’s carrying frog” for the new species and the common name of “carrying frogs” for all *Stefania* species. The proposed common name in Spanish is “Rana *Stefania* de Brewer,” in accordance with names for other *Stefania* proposed by Barrio-Amorós (1998).

Remarks.—The holotype is somewhat dehydrated. The prominence of the frontoparietal ridges, the canthus rostralis, and concavities of the loreal and interorbital regions may be the result of dehydration. We decided not to dissect the only known specimen in order to avoid damage. Thus, the sex is unknown.

DISCUSSION

As previously noted, Rivero (1970) assigned the species of *Stefania* known at that time to two species groups (*S. evansi* and *S. goini* groups). Myers and Donnelly (1997) commented that Duellman and Hoogmoed (1984)

did not explicitly assign their new species to either of Rivero’s groups, but included the groups in their general discussions and summary. In their generic revision and description of five species, Señaris et al. (1996) placed their species in Rivero’s groups. *Stefania tamacuarina* seems to be a member of the *S. evansi* group (Myers and Donnelly, 1997). *Stefania breweri* can be placed in the *S. evansi* group because of its head proportions and its mid-elevation habitat. Therefore, with the new taxa, Rivero’s groups consist of the *S. evansi* group containing *S. ackawaio*, *S. ayangannae*, *S. breweri*, *S. evansi*, *S. marahuaquensis*, *S. percristata*, *S. riae*, *S. roraimae*, *S. scalae*, *S. tamacuarina*, and *S. woodleyi* (Fig. 5); and the *S. goini* group containing *S. coxi*, *S. ginesi*, *S. goini*, *S. oculosa*, *S. riveroi*, *S. satelles*, and *S. schuberti* (Fig. 6).

No species known from Venezuela are also known from other countries, with the exception of *S. scalae* in Guyana (MacCulloch and Lathrop, 2002). *Stefania evansi* has been listed continuously as present in Venezuela by La Marca (1992, 1997) and Barrio-Amorós (1998), perhaps due to the confusion with *S. scalae*. However, there are no known records of *S. evansi* from Venezuela, and it should be removed from any lists until its presence in Venezuela is confirmed. Although recent exploration has resulted in the discovery of *Stefania* in many mountains of southern Venezuela, still more exploration is needed. For example, *S. tamacuarina*, described from Pico Tamacuari (Serranía de Tapirapecó), Venezuela, probably also exists on the Brazilian side of the serranía. Likewise, *S. roraimae* is so far known only from the Guyanese side of the base of Roraima tepui, but it likely occurs in Venezuelan and Brazilian sides as well. With the recent and outstanding discovery of seven species of *Stefania*, mostly syntopic and inhabiting the same tepui in Guyana (MacCulloch and Lathrop, 2002), we can expect more cases of sympatry in Venezuela, where only two tepuis are known to be inhabited by more than one species: Cerro Jaua, where *S. oculosa* and *S. percristata* live in sympatry (Señaris et al., 1996), and Cerro Duida, where *S. marahuaquensis* and *S. goini* are syntopic (Señaris et al., 1996).

Biogeography.—Cerro Autana is located in the northwestern part of Estado Amazonas,

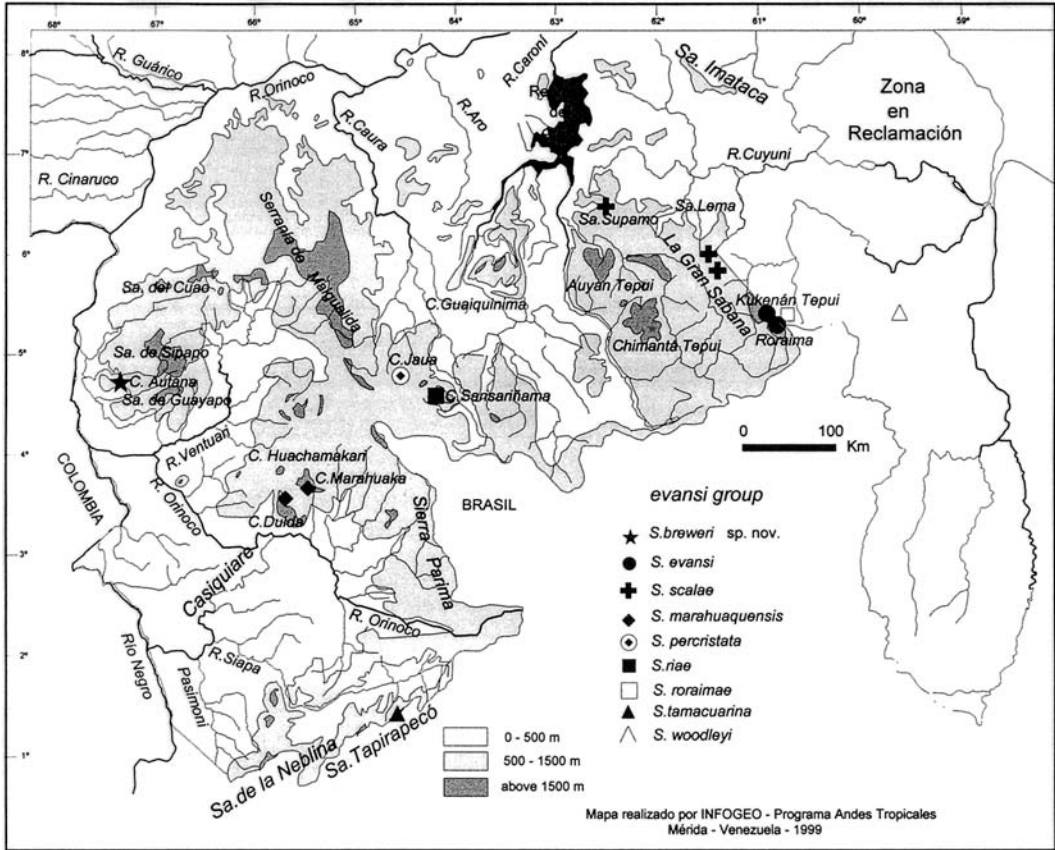


FIG. 5.—Geographic distribution of *Stefania evansi* group in Southern Venezuela. The star indicates the type locality (Cerro Autana) of *Stefania breweri* sp. nov.

Venezuela. It is the westernmost locality for the genus, 45 km east of the Río Orinoco, which marks the Venezuelan-Colombian border. West of the Orinoco, in Colombia, the landscape is a vast lowland plain covered with savannas and rainforest, with some uplands to the west (Serranía de Chiribiquete, maximum elevation slightly above 1000 m; and Serranía La Macarena, reaching 2500 m), each approximately 760 km from Autana. *Stefania* is not known from those serranías, and it is unlikely that it occurs there or in any of the lowlands in between. The closest locality from which a species of *Stefania* has been reported is Cerro Huachamacari (*S. goini*), 200 km to the southeast of Cerro Autana; the two highlands are separated by the lowland savannas of the Río Ventuari Valley. The discovery of *Stefania* on a northwestern tepui is surprising because of the great distance between Autana and the

other known localities of the genus, and also because *Stefania* was not found on Yavi or Yutaje-Corocoro (Myers and Donnelly, 1996, 2001). Undoubtedly other species of *Stefania* are still to be discovered.

RESUMEN

Describimos una nueva rana del género *Stefania* de la cumbre del Cerro Autana, estado Amazonas, Venezuela, siendo la especie más occidental hasta ahora conocida del género, a 200 km NW del Cerro Huachamacari, el punto más cercano de donde se conoce otra especie. La nueva especie se distingue del resto de especies del género por la combinación de los siguientes caracteres: crestas frontoparietales presentes pero reducidas, palmeadura pedial basal, discos en manos y pies pequeños, ausencia de tubérculos en la región post-timpanica, cabeza tan larga como

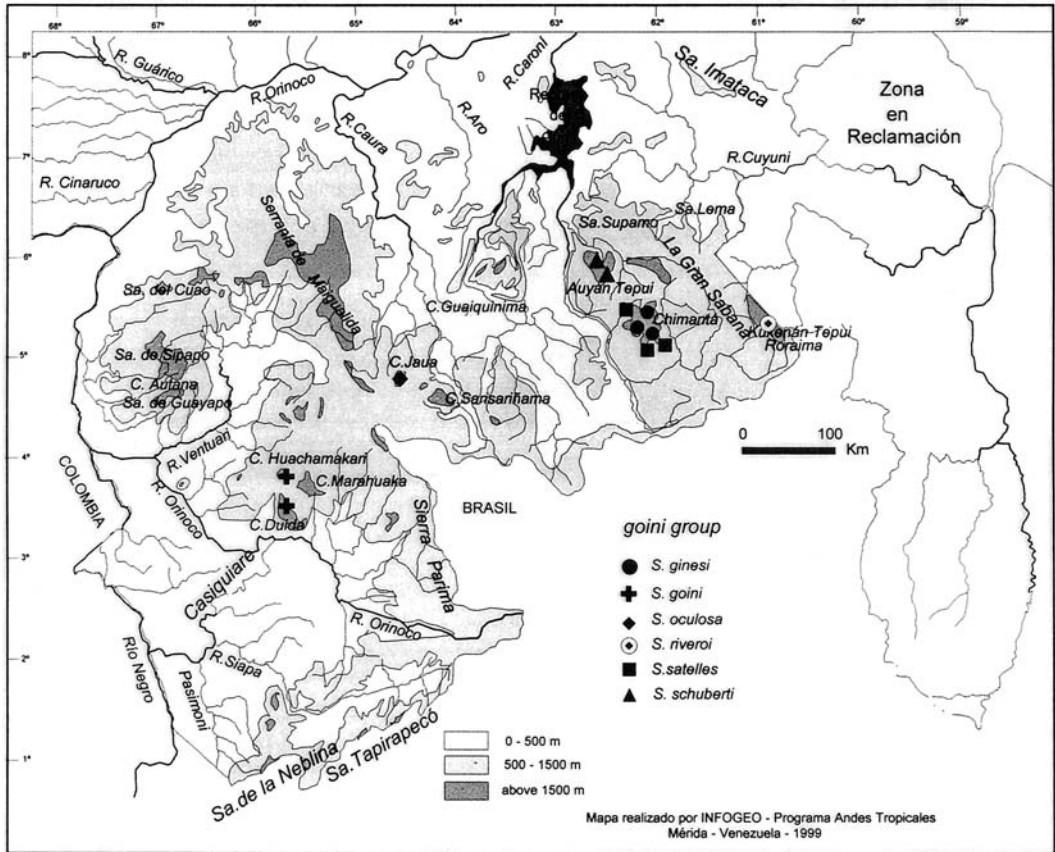


FIG. 6.—Geographic distribution of *Stefania goini* group in Southern Venezuela.

ancha. De acuerdo con estos caracteres, la especie es asignada al grupo *S. evansi* de Rivero.

Acknowledgments.—We are indebted to C. Brewer-Caías for the specimen and his encouragement; the Programa Andes Tropicales (PAT) for allowing Barrio-Amorós access to its facilities in Mérida; M. Molinillo (INFOGEO) for help preparing the maps; J. Brewer-Caías for arranging the transparency of *Stefania*; A. Orellana for his help in translating the text; A. Chacón for the drawings; A. Rodríguez-Acosta, R. Guerrero, W. E. Duellman, and M. Hoogmoed for their helpful and valuable comments on versions of the manuscript; and R. MacCulloch for sharing information and literature on the genus and its biogeography and natural history.

LITERATURE CITED

- BARRIO-AMORÓS, C. L. 1998. Sistemática y Biogeografía de los anfibios (Amphibia) de Venezuela. *Acta Biologica Venezuelica* 18:1–93.
- BOULENGER, G. A. 1904. Description of a new tree frog of the genus *Hyla*, from British Guiana, carrying eggs on the back. *Proceedings of the Zoological Society of London* 1904:106.
- DUELLMAN, W. E., AND M. S. HOOGMOED. 1984. The taxonomy and phylogenetic relationships of the hylid frog genus *Stefania*. University Kansas Museum Natural History Miscellaneous Publication 75:1–39.
- FRANK, N., AND E. RAMUS. 1995. A Complete Guide to Scientific and Common Names of Reptiles and Amphibians of the World. NG Publishing, Pottsville, Pennsylvania, U.S.A.
- FROST, D. 2000. Amphibian species of the world. An online reference. <http://research.amnh.org/herpetology/amphibia/index.html>
- GORZULA, S., AND J. C. SEÑARIS. 1998. Contribution to the herpetofauna of the Venezuelan Guayana. I. A data base. *Scientia Guianae* 8:1–267.
- HUBER, O., AND C. ALARCON. 1988. Mapa de Vegetación de Venezuela, 1:2,000,000. Ministerio del Ambiente y de los Recursos Naturales Renovables and The Nature Conservancy, Caracas, Venezuela.
- LA MARCA, E. 1992. Catálogo taxonómico, biogeográfico y bibliográfico de las ranas de Venezuela. Cuadernos

- Geográficos Universidad de Los Andes, Mérida, Venezuela.
- . 1997. Lista actualizada de los anfibios de Venezuela. Pp. 103–120. *In* La Marca (Ed.), Vertebrados Actuales y Fósiles de Venezuela. Museo de Ciencia y Tecnología de Mérida, Venezuela.
- MACCULLOCH, R., AND A. LATHROP. 2002. Exceptional diversity of *Stefania* (Anura: Hylidae) on Mount Ayanganna, Guyana: three new species and new distribution records. *Herpetologica* 58:327–346.
- MYERS, C. W., AND M. A. DONNELLY. 1996. A new herpetofauna from Cerra Yavi, Venezuela: first results of the Robert G. Goelet American Museum – TERRAMAR expedition to the northern tepuis. *American Museum Novitates* 3172:1–56.
- . 1997. A tepui herpetofauna on a granitic mountain (Tamacuari) in the borderland between Venezuela and Brazil: Report from the Phipps Tapirapecó Expedition. *American Museum Novitates* 3213:1–71.
- . 2001. Herpetofauna of the Yutaje-Corocoro massif, Venezuela: second report from the Robert G. Goelet American Museum – TERRAMAR expedition to the northwestern tepuis. *Bulletin of the American Museum of Natural History* 261:1–85.
- MYERS, C. W., AND W. E. DUELLMAN. 1982. A new species of *Hyla* from Cerro Colorado, and other tree frog records and geographical notes from western Panama. *American Museum Novitates* 2752:1–32.
- RIVERO, J. A. 1961. Salientia of Venezuela. *Bulletin Museum Comparative Zoology* 126:1–207.
- . 1968. Notes on the genus *Cryptobatrachus* (Amphibia, Salientia) with the description of a new race and four new species of a new genus of hylid frogs. *Caribbean Journal Science* 6:137–149.
- . 1970. On the origin, endemism and distribution of the genus *Stefania* Rivero (Amphibia, Salientia) with a description of a new species from southeastern Venezuela. *Boletín Sociedad Venezolana Ciencias Naturales* 28:456–481.
- RUTHVEN, A. G. 1922. The amphibians and reptiles of the Sierra Nevada de Santa Marta, Colombia. *Miscellaneous Publications University Michigan Museum Zoology* 8:1–69.
- SEÑARIS, C. J., J. AYARZAGÜENA, AND S. GORZULA. 1996. Revisión taxonómica del género *Stefania* (Anura: Hylidae) en Venezuela, con la descripción de cinco nuevas especies. *Publicaciones Asociación Amigos Doñana* 7:1–56.
- STEYERMARK, J. A. 1974. The summit vegetation of Cerro Autana. *Biotropica* 6:7–13.

Accepted: 30 April 2003

Associate Editor: Joseph Mendelson III

APPENDIX I

Specimens Examined

Stefania riae: Venezuela: estado Bolívar: Sima Mayor, Sarisariñama (EBRG 4533–42).

Stefania scalae: Venezuela: estado Bolívar: Salto El Danto, Sierra de Lema (CVULA 3183); km 112 (EBRG 980), km 117 (EBRG 3440), and km 125 of the road from El Dorado to Santa Elena de Uairén (MBUCV 6573), 860–1025 m, and another adult individual examined alive and photographed from Cerro Santa Rosa, Serranía del Supamo, 600 m.

Stefania schuberti: Venezuela: estado Bolívar: eastern side of the summit of the Auyán-tepui, 1750 m (EBRG 3000, 3001; MBUCV 3039).