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Description of A new species of the genus *Adenomera* (Amphibia, Anura, Leptodactylidae) from French Guiana

Renaud Boistel [1], Jean-Christophe de Massary [2] and Ariadne Angulo [3,4]

[1] *Université Paris Sud. Centre Scientifique d'Orsay, Laboratoire des Mécanismes de Communication animale, NAM CNRS UMR 8620. Bâtiment 446, 91405 Orsay cedex, France.*
[2] *4, rue des Tilleuls, 95170 Deuil-la-Barre, France*
[3] *Conservación Internacional Carrera 13 # 71-41 Bogotá, Colombia*
[4] *Departamento de Herpetología, Museo de Historia Natural de San Marcos, Apartado 14-0434, Lima, Perú*

Abstract. We describe a new species of the genus *Adenomera* from French Guiana. Collecting conditions, details about the localities and microhabitats are given. The advertisement call was recorded and is herein analyzed and described. Morphological and bioacoustic comparisons are drawn with other species of the genus. The new species is readily distinguished from other taxa by its distinctive coloration pattern, the occurrence of dorsolateral ridges and inguinal glands, and by the longer duration of the notes of its advertisement call. The taxonomy of *Adenomera* is evaluated with regard to current available knowledge.

Key words. *Adenomera heyeri* n. sp., Leptodactylidae, French Guiana, morphology, advertisement call

INTRODUCTION

The Neotropical anuran genus *Adenomera* Steindachner, 1867 was resurrected by Heyer (1974) for *the Leptodactylus marmoratus* group; this author recognized five species: *Adenomera andreae* (Müller, 1923), *A. bokermanni* (Heyer, 1973), *A. hylaedactyla* (Cope, 1868), *A. marmorata* Steindachner, 1867 and *A. martinezi* (Bokermann, 1956). In 1975, Heyer (1975) described a sixth species, *A. lutzi* Heyer, 1975. Recently, a seventh species, *A. diptyx* (Boettger, 1885), has been resurrected (De la Riva, 1996) and *A. araucaria* Kwet and Angulo, 2002 is described from southern Brazil (Kwet and Angulo, 2002). To date, eight nominal species are recognized (Frost, 2004) , although there is evidence to support a much higher species diversity in this group of frogs (Angulo, 2004). *A. andreae* and *A. hylaedactyla*, the two nominal species with widespread distributions throughout the Amazon Basin, have been previously reported in French Guiana (Heyer, 1973). Their calls are frequently heard in rainforest and associated habitats and it is possible to distinguish these

two species on the basis of their advertisement calls (Rodríguez and Duellman, 1994). The advertisement call presents a good potential as a means to resolve the systematics of this genus (Heyer, 1984; Angulo et al, 2003).

Three specimens of an unknown species of *Adenomera* were found at the field station of Saint-Eugène, French Guiana (Fig. 1). Moreover, four additional specimens of this new species have been collected at the field station of Nouragues, in the same country. Herein we describe this new species.

The advertisement calls of five nominal species of the genus *Adenomera*, *A. hylaedactyla*, *A. andreae*, *A. araucaria* and *A. marmorata* have been previously described (Heyer, 1973; Straughan and Heyer, 1976; Heyer et al., 1990; Márquez et al., 1995; Zimmerman and Bogart, 1984; Kwet and Angulo, 2002). In addition to the description of the new spe-

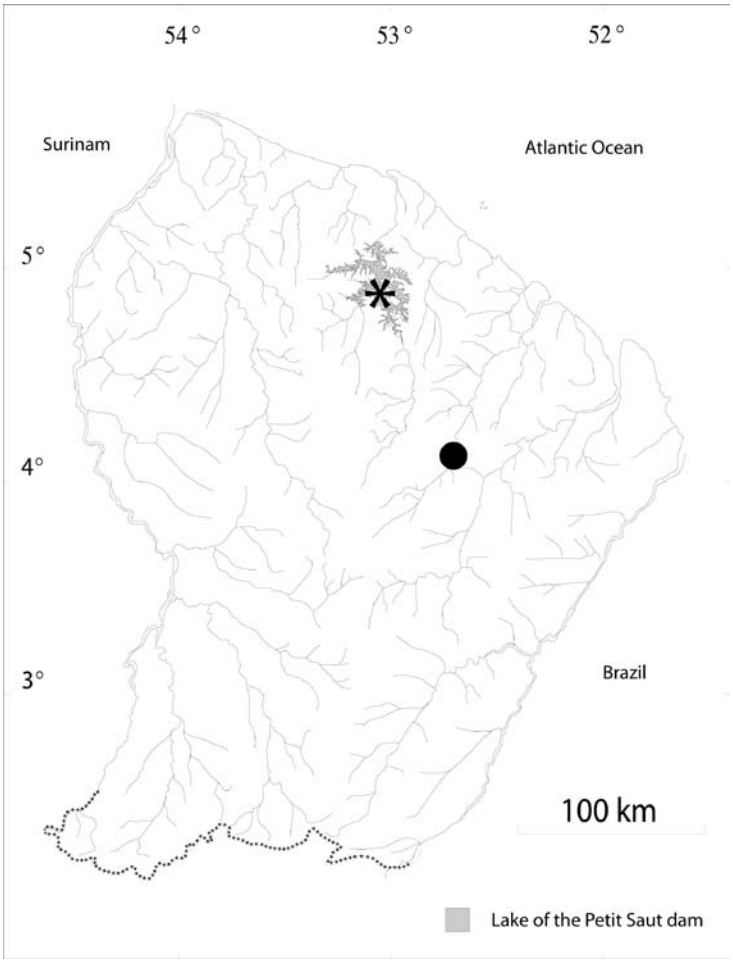

Fig. 1. Map of French Guiana with the two localities known for *Adenomera heyeri*. The asterisk indicates the type-locality (Saint-Eugène field station), the circle the Station of Nouragues.

cies, we take this opportunity to further analyze of the known vocalizations in order to find discriminating parameters for the genus.

MATERIALS AND METHODS

Morphological Analysis

Specimens used in the description of the new species are deposited at the Museum national d'Histoire naturelle (MNHN), Laboratoire de Zoologie (Reptiles et Amphibiens), Paris. Other museum acronyms follow Leviton and Gibbs (1988).

Specimens were fixed in 10 % formalin and preserved in 70 % ethyl alcohol. All measurements were taken after fixation. Abbreviations used in the measurements of the seven specimens are EL (horizontal eye length), EN (distance from anterior edge of eye to nostril), FLL (forelimb length, from elbow to base of outer tubercle), FTL (fourth toe length), HL (head length), HW (head width), IN (internarial distance), IUE (minimum distance between upper eyelids), SVL (snout-vent length), TD (tympanum diameter), TL (tibia length), TFL (third finger length), and UEW (maximum width of upper eyelid). Measurements were taken either with a caliper to the nearest 0.1 mm or with a stereomicroscope equipped with an ocular micrometer under magnifications of 6x, 12x, 25x and 50x. We also counted the number of vomerine teeth (VT), both at the left (L) and right (R) side. An X-ray was taken of one paratype in ventral view to examine osteological characters.

Data Acquisition and Sound Analysis

The origin of the data and the recording conditions are summarized in appendix 1. Analog signals were digitized using a 16-bit Digigram PCcard acquisition card at a sampling frequency of 16000 Hz. Additionally, we sampled at 32000 Hz in order to observe harmonic structure. Recordings were analyzed with analytical software Syntana (Aubin, 1994). Fast Fourier transforms (FFTs, window size = 4096 data points, Δf = 120 Hz) were calculated. For the spectrum analysis, we used an FFT (window size = 2048 data points, Δf = 8 Hz) at the middle of the note for each selected call of the recorded series. The duration of signals and silences was measured on the oscillogram of all signals. Their amplitude envelope and instantaneous frequency function were calculated by means of the Hilbert transform (see Mbu-Nyamsi et al., 1994). We used an envelope (the envelope was digitally filtered using FFTs window size = 4096 data points, overlapping 97-100 %, band pass = 0-250 Hz) of the signal for the analysis of the structure of AM (amplitude modulation) and the instantaneous frequency for analysing the FM (frequency modulation) parameters of the signal. Because this method provides the instantaneous frequency, it allows us to obtain fine details not detected by a classic FFT as, for instance, the frequency sweeps.

The terminology follows Boistel and Sueur (1997), Beeman (1998), Gerhardt (1998), and Hartmann (1998). We took the following measurements: DSQ (duration of sequences), DN (duration of notes), DS (duration of silences), DI (duration of intra-signal variation of amplitude), f0 (fundamental frequency), 2f0 (twice the fundamental frequency), FM (frequency modulation) and AM (amplitude modulation). We used the NR (note rate, which is the number of notes for each unit of time) and rhythm (ratio of silence and sound duration), according to Aubin and Brémond (1983). For *Adenomera araucaria*, we used the data on advertisement calls provided by Kwet and Angulo (2002).

RESULTS

***Adenomera heyeri* n. sp.** (Figs. 2-5)

Diagnosis

The new species is distinguished from all other species by its advertisement call and the following combination of characters: (1) two pairs of dorsolateral folds present; (2) smooth skin on lower surface of foot or with a few small white tubercles; (3) throat and belly of males yellow; (4) tarsal fold present and slightly marked.

Adenomera heyeri differs from *A. martinezi* in lacking four longitudinal rows of symmetrically arranged dark spots on its dorsal surface. This news species is distinguished from *A. araucaria* by its larger size and by its advertisement call. *Adenomera bokermanni* and *A. lutzi* have a profusion of white-tipped tubercles on the lower surface of the tarsus and the sole of foot, whereas those parts are smooth, or with some very scant, small tubercles in *A. heyeri*. The vocal slit is elongate, slightly oblique to the jaw or parallel to the jaw in *A. marmorata*, whereas *A. heyeri* has small vocal slits, present just behind the angle of the jaw. *Adenomera heyeri* has two pairs of slightly discontinuous parallel folds starting behind the eyes and running toward the posterior part of the back; these are absent in *A. andreae*; in addition, the signal duration is about 2.5 times longer in *A. heyeri* than it is in *A. andreae* (Table 1). *Adenomera heyeri* is distinct from *A. hylaedactyla* by having the head as wide as long, its snout is, from above, nearly rounded versus subovoid, pulses are absent and note duration is longer (Tables 1 and 2).

Holotype. MNHN 1999.8331 (Figs. 2, 4), adult male collected at the MNHN field station of Saint-Eugène (4°51'N; 53°3'W, 65 m elevation), 23 km by air from the newly built Petit Saut Dam, Courcibo River, principal tributary of the Sinnamary River**,** French Guiana, leg. Renaud Boistel, 24 April 1998.

Paratypes. MNHN 1997.2273, adult female, and MNHN 1998.322, adult male, from the type locality, leg Jean-Christophe de Massary, 2 April 1997 and 13 April 1998; MNHN 1999.8301, adult male, and MNHN 1999.8302-8304, three juveniles, from the station of Nouragues (4°5' N, 52°41' W, 110 m elevation), 8 km N of Saut Pararé, Arataye river, French Guiana, leg. Renaud Boistel, May 1999.

Description of Holotype

Snout from above nearly rounded, in profile obtuse; canthus rostralis straight, indistinct; loreal region acute, head wider than long; nostrils anterolateral, closer to snout tip than to eyes. Interorbital space flat, twice as wide as upper eyelid, slightly longer than the internarial distance; tympanum distinct, its maximum diameter about 2/3 of eye diameter; pupil horizontal and elliptic; vomerine ridges present, in short transverse series L9/R8, separated by a distance smaller than the length of one tooth row; maxillary teeth present; tongue rounded, not emarginated on anterior edge; the elongated vocal slits are present,

Table 1. Advertisement call measurements for *Adenomera heyeri, A. andreae, A. hylaedactyla* and *A. marmorata.* Data for *A. heyeri* originate from the type specimens (MNHN 1999.8331). Asterisks indicate that the extraction of measurements was not possible in two (long distance recordings) specimen. Abbreviations used are: n = number of specimens, DSQ = duration of sequences, DN = duration of notes, DS = duration of silences, DI = duration of intra-signal variation of amplitude, NR = note rate in number of notes per second (NN/s), f0 = fundamental frequency, 2f0 = twice the fundamental frequency, FM = frequency modulation, AM = amplitude modulation.

	A.heyeri	*A. andreae*	*A. hylaedactyla*	*A. marmorata*
n	1	3	1	1
DSQ (s)	30.2	39.6	3.7	17.2
DN (ms)	154.2 ± 13.5 (136.87-184.5) n = 17	66.5 ± 10.9 (44.5-85.7) n = 45	49.7 ± 2.5 (45.0-52.7) n = 16	45.9 ± 2.9 (42.2-55.6) n = 16
DS (ms)	1722.4 ± 418.3 (1198.8-2446.1) n = 16	874.8 ± 149.0 (643.3 - 1264.9) n = 42	193.7 ± 21.5 (162.7-223.8) n = 15	1096.3 ± 154.6 (877.1-1444.7) n = 15
DI (ms)	6.8 ± 2.1 (3.9-16.9) n = 351	4.4 ± 0.8 (2.1 - 7.9) n = 336	8.1 ± 2.3 (5.2 - 15.4) n = 96	/
NR (NN/s)	0.56	1.13	4.32	0.93
Rhythm	10.51	11.74	3.66	22.38
f0 (Hz)	1856 ± 31 (1815-1878) n = 17	2438 ± 157 (2316-2692) n = 45	2107 ± 19 (2091-2128) n = 16	4790 ± 11 (4782-4808) n = 16
2f0 (Hz)	3657 ± 61 (3568-3844) n = 17	4871 ± 359 (4557-5493) n = 45	4341 ± 32 (4282-4407) n = 16	/
Period of sinusoidal FM (ms)	13.1 ± 2.6 (9.2-25.2) n = 162	11.5 ± 2.7* (6.9-22.6) n = 64	8.1 ± 2.3 (5.2-15.4) n = 96	/
Linear FM (Hz)	399 ± 55 (300-487) n =17	629 ± 105 (451-789) n =45	453 ±2 3 (401 - 484) n =15	572 ± 66 (463 - 689) n =16
AM (Hz)	/	210 ± 24 (155.5-278) n =45	124 ± 16 (93.5-144) n =16	/

supratympanic fold distinct, although weakly or barely developed, ranging from eye to angle of jaw. Arms short with robust forearms, lacking forearm tubercules (as found in *Pseudopaludicola*); forearms as long as hands; fingers elongate, thin, without dermal fringe or webbing; tips of fingers rounded, flattened, without grooves but with dorso-terminal ridges at the level of digit articulation; finger lengths in increasing order: IV ≤ II = I < III; subarticular tubercles well developed, oblong or ovoid; inner and outer metacarpal tubercles large, prominent, outer larger than inner, shape of inner oblong, that of outer long; palmar tubercles absent; supernumerary tubercles distinct, small, rounded; sole of hand

Table 2. Principal parameters characterizing the advertisement call of four *Adenomera* species (see materials and methods for the parameter definitions).

	A. heyeri	*A. andreae*	*A. araucaria*	*A. hylaedactyla*	*A. marmorata*
Number of harmonics	2 to 6	1 to 7	3 to 6	2	0
Dominant frequency	2f0	2f0	2f0	2f0	f0
FM	sinusoidal & linear	sinusoidal & linear	linear	sinusoidal & linear	linear
Nb of oscillations in sinusoidal FM	9,5	4	0	6,2	0
AM	no	yes	yes	yes	no
Pulses	0	0	0	4	0
Tempo	slow	average	slow-average	fast	average
Rhythm	medium	medium	strong	weak	strong

Fig. 2. Overview of the type specimen in its natural habitat; Saint-Eugène field station, May 1998 (Photo R. Boistel).

smooth. Shank longer than thigh and shorter than distance from base of internal metatarsal tubercle to tip of toe IV; relative length of toes, in increasing order: I ≤ V < II < III < IV. Toe tips bulbous, spatulate, broader than toe width just behind tips; dorso-terminal toe ridges at level of tarsal articulation not developed into fringes; subarticular tubercles well developed, ovoid; outer metatarsal tubercle round, smaller than ovoid, flattened inner tubercle; tarsal fold slightly marked; no metatarsal fold; outer tarsus absent; supernumer-

Fig. 3. Left foot (1) and left hand (2) of *Adenomera heyeri* (paratype MNHN 1999.8301).

ary tubercles on sole of foot hardly distinct, small, rounded. Top of head and eyelids, forearms and all the ventral surface smooth. Two pairs of slightly discontinuous parallel folds starting behind the eyes and running toward the posterior part of the dorsum. Occipital region, dorsum, and dorsal surfaces of forearms, thighs and shanks covered with pustules. Upon fixation and preservation both pustules and dermal folds are considerably less marked or lost altogether. Two small lumbar glands present. It is possible to observe a small supralabial gland at each side of the jaw.

Coloration in Life

This species can be easily identified by its coloration. The back is overall brown but dark markings occur: a mid-dorsal line begins at the snout, is slightly enlarged around the interorbital area, continues along the back tapering, and disappears around the sacral region. Two dark stripes (one on either side) with unclear limits, start from the nostrils and continue dorsolaterally following the dermal folds, stopping before the two small, well defined, black lumbar glands. One short dark, oblique lateral band begins at the dermal fold and reaches the inguinal region; one dark stripe starts at the supratympanic fold and disappears on the lower part of the flanks. The background color is light brown. The sides of the head are dark; on each side, a whitish mark starts from under the posterior part of the eye to the insertion of the forelimb; this mark includes the supralabial gland. The lower lip is bordered by dark brown. The gular region is slightly yellowish with small brown spotted marks. The belly and the ventral side of the limbs are uniformly yellowish in life but whitish in preserved specimens. The soles of the feet and the palms of the hands are brown. The iris is bronze with black reticulations; the palpebral membrane is translucent and is bordered in its upper part by a black streak. The forelimbs and hindlimbs are light brown dorsally with, respectively, two and three cross bars. Upon preservation, the coloration is overall conserved.

Measurements of Holotype (in mm)

Snout vent length 22.5, head length 9.6, head width 9.2, interocular distance 2.5, shank length 10.8, length of fourth toe 5.2, eye diameter 2.3, eye-nostril distance 2.0, internarial distance 2.2.

Variation

Measurements of seven specimens are given in Table 3. According to data currently available, *Adenomera heyeri* can reach a maximum SVL of about 26 mm in males and the unique female of our sample measures 23.1 mm.

The coloration is similar among all specimens. The gular region is a dull white in the female and is slightly yellowish with small brown spotted marks in the male. The belly and the ventral portions of the upper limbs are uniformly whitish to yellowish in preserved specimens. The dermal folds of some fixed specimens are less marked, and sometimes totally disappear after fixation. Juveniles show a slightly different coloration at the level of the upper lip, which is white with brown bands. Overall, morphology and coloration are quite uniform.

Secondary Sexual Characters

Males have a vocal apparatus, consisting of a single vocal sac and two small vocal slits present just behind the angle of the jaws; their upper lip is more developed than in females; there are no nuptial pads. The snout from above is nearly rounded to rounded, in profile it is acuminate in our single female and obtuse in males.

Advertisement Call

All call data herein refer to the holotype. The advertisement call of *Adenomera heyeri* can be detected by the human ear at over 50-60 metres. Temporal features of adver-

Table 3. Size measurements on the seven known specimens of *Adenomera heyeri*. The holotype (MNHN 1999.8331) bears an asterisk (see materials and methods for abbreviations of the measurements).

	1997.2273	1998.0322	1999.8301	1999.8302	1999.8303	1999.8304	1999.8331*
SEX	F	M	M	J	J	J	M
SVL	23.1	23.6	25.8	10.0	10.3	10.8	22.5
HL	9.1	9.7	11.0	4.2	4.2	4.6	9.6
HW	10.7	9.8	10.3	4.8	4.8	4.5	9.2
IN	2.1	2.7	2.5	1.2	1.1	1.3	2.2
EN	1.9	1.9	2.0	0.9	1.0	0.9	2.0
EL	2.8	2.6	3.0	1.3	1.3	1.7	2.3
UEW	1.5	1.7	1.7	0.9	0.9	1.0	1.5
IUE	2.8	2.8	3.3	1.4	1.4	1.7	2.5
TD	1.5	1.6	2.0	0.4	0.4	0.5	1.5
FLL	5.5	5.9	5.9	2.3	2.2	2.4	5.4
TFL	5.2	5.4	5.4	1.7	-	-	5.2
TL	11.2	10.8	10.8	4.5	4.4	5.2	10.8
FTL	10.5	11.3	11.0	4.1	-	-	11.2
VT	L10/R9	L8/R9	L10/R9	L5/R5	L5/R5	L5/R5	L9/R8

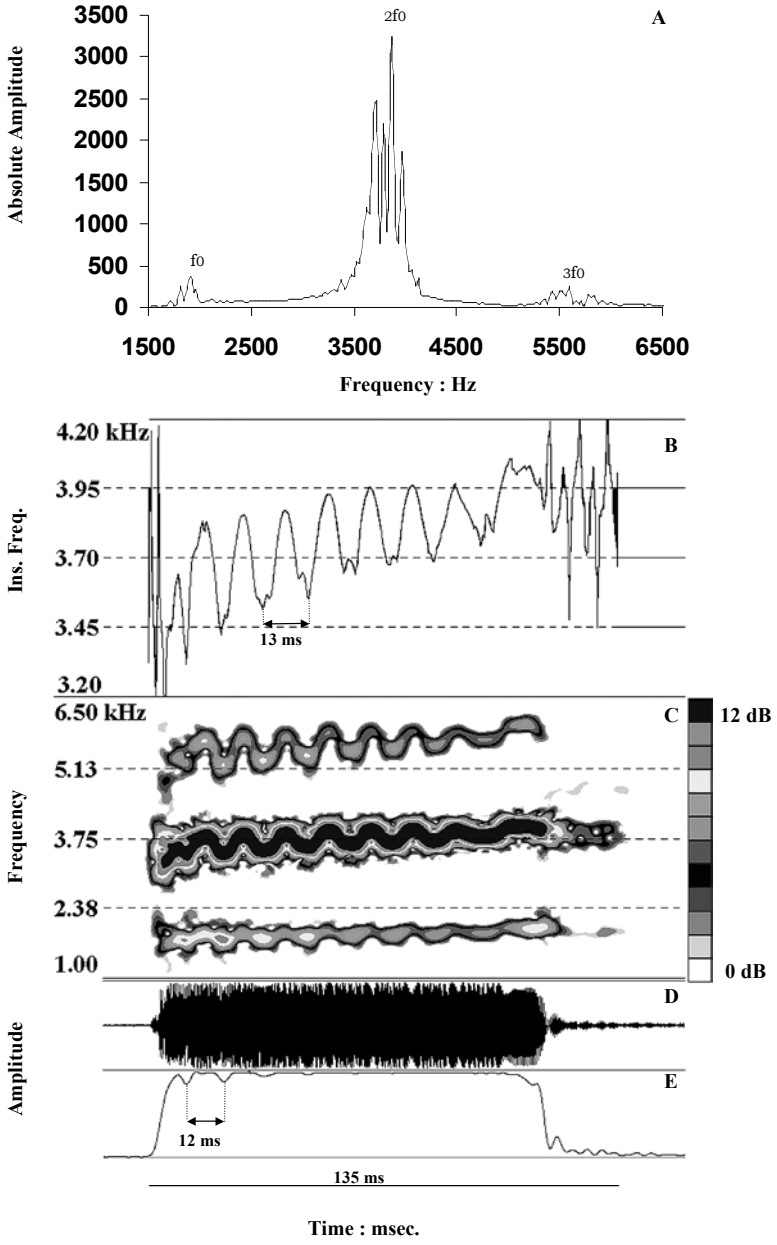

Fig. 4. Graphic representation of the advertisement call of *Adenomera heyeri* (holotype MNHN 1999.8331): (A) spectrum, the two peaks correspond to the fundamental frequency (f0) and the first harmonic (2f0); (B) instantaneous frequency by Hilbert transform; (C) Sonogram with a palette of 12 colors of depicting different intensities, one color represents 3 dB, white color is a minimum intensity and gray color on top is maximum intensity; (D) oscillogram; (E) envelope; two periodic variations are detected, 6 and 12 ms.

tisement calls are given in Table 1. The call of *A. heyeri* is distinct from that of the other three species in all parameters (see Tables 1 and 2). The calling sequence is a repetition of identical notes (Figs. 4 C, D, E), with each call having an average duration of 154 ms, emitted at a note rate of 0.56 notes/s and a rhythm of 10.51. The duration of silences is about 1722 ms. The durations of notes and silences in *A. heyeri* are longer than those of the other species examined and its note rate is the slowest; the rhythm is similar to that of *A. andreae*. The envelope (Fig. 4E) shows one periodical pattern of variation in amplitude with a duration of 13 ms. With regard to spectral features (Figs. 4 A, B, C), a fast FFT indicates that, within the serial harmonic, the average fundamental frequency (f0) is 1856 Hz (Figs. 4 A, C); this frequency is lower than in the other species dealt with here (Table 2). The dominant frequency is located at 3657 Hz (2f0). In all other species of *Adenomera* the dominant frequency is 2f0, with the exception of *A. marmorata*, in which the dominant frequency is f0. The other peaks near the f0 and 2f0 are understood as an effect of frequency modulation (FM). Notes were found to have a series of six distinguishable harmonics (Table 2). The sonogram (Fig. 4 C) and analysis by using the Hilbert transform, which gives the instantaneous frequency (Fig. 4 B), show a frequency modulation (FM). The FM is linear upward, rising from 3422 to 3821, and with a sinusoidal oscillation repeated 9.5 times in one note; it has an W shaped profile in the dominant frequency (Fig. 4 B), differing from *A. araucaria* and *A. marmorata* by the absence of a sinusoidal FM. The discontinuities of the frequency curve coincide with the variation of instantaneous amplitude, which has a periodicity of 12 ms (Figs. 4 B, E). The call of *A. heyeri* differs from the calls of *A. andreae* and *A. hylaedactyla* by the absence of AM.

Distribution and ecology

To date, *Adenomera heyeri* is only known from its type locality and a nearby site (see Holotype and Paratypes) (Fig. 1). Few data are available about the species' ecology. It seems to have a nocturnal activity in terrestrial environments. According to observations made by the first author, males start their calling activity during dusk in the rainy season (April-May). Specimens have been found both in moist low elevations and on the summit of small hills (about 120 m elevation), with or without rocks, in drier conditions. Though one of us (JCDM) spent about 17 months in the field (i.e. 3 dry seasons and 3 rainy seasons) using pitfall traps continuously, this species was never found during the dry season. Moreover, it is interesting to note that all specimens were collected in April or May only. These facts may probably reflect an increase in activity at the onset of the rainy season, possibly for reproductive purposes. In every case, *A. heyeri* seems to have a "secretive" life, and is therefore difficult to find.

Etymology

This species is dedicated to W. Ronald Heyer for his important contributions to leptodactylid frog studies of South America and in particular the genus *Adenomera*.

DISCUSSION

Systematic issues in *Adenomera* have been difficult to resolve. Morphologically, most species are cryptic and Heyer (1984) suggested that topotypic advertisement calls could be used to resolve their taxonomy. Advertisement call characters in anurans are highly species-specific prezygotic isolation mechanisms and as such are excellent indicators of species identity, as accumulated evidence suggests (e.g. Heyer et al., 1996). In the case of cryptic species, once it is possible to associate a frog with a particular call, it is also possible to search for correlates between this call and distinctive morphological characters. *Adenomera heyeri*

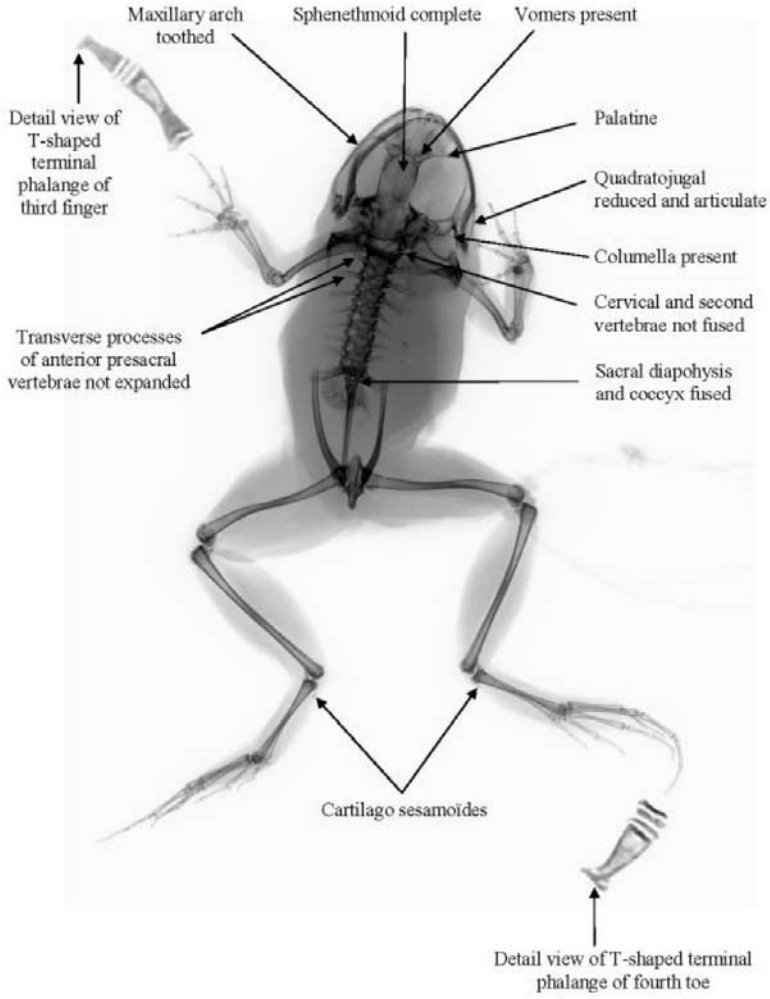

Fig. 5. X-ray picture of *Adenomera heyeri*, male paratype MNHN 1998.322, with details about the phalanges of both the right hand and the left foot. Note T-shaped tips of phalanges.

was sufficiently divergent morphologically to immediately suspect it was a new species, and the distinctiveness of its advertisement call corroborated this. However, in other species of *Adenomera*, the morphology is not conspicuously distinct, as in the case of *A. andreae* and *A. hylaedactyla.* Angulo et al. (2003), using acoustic characters, found that these two *Adenomera* represent four taxa at a locality in Amazonian Peru.

Heyer (1974) examined the relationships of frogs of the *marmoratus* group of *Leptodactylus,* and redefined *Adenomera* as a valid genus with a number of characters distinguishing it from other leptodactylids. Although superficially similar to *Pseudopaludicola*, the new species has more attributes in common with *Adenomera* than with any other member of the leptodactylines [characters such as T-shaped terminal phalanges (Fig. 5), sternal style and presence of tarsal fold], which is the reason for its placement in this genus. However, there are still a number of characters which are unknown in the new species (e.g. characters of a myological nature, detailed osteological data or reproductive mode). Moreover, one character state observed in some specimens of *A. heyeri* is different from what was previously known for *Adenomera*, i.e. sole of foot smooth. We will not rule out that future analyses of genera may reveal a placement of *A. heyeri* basal to or out of *Adenomera.* Nevertheless, according to the best of our knowledge, it is currently best placed within this genus.

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Appendix 1. Summary of the origin and condition of recordings for the different frog species considered.

	A. andreae	*A. hylaedactyla*	*A. marmorata*	*A. heyeri*
Data taken by	R. Boistel	A. Angulo	W.R. Heyer	R. Boistel
Date	20 April 1998 (18:50-19:20 h)	26 January 1999 (19:11 h)	12 December 1976	24 April 1998 (18:50 h)
Locality	Saint-Eugène (French Guiana)	Tambopata National Reserve (Peru)	Boracéia (Brazil)	Saint Eugène (French Guiana)
Tape recorder	DAT AIWA HDS1000	Walkman SONY D6C	Uher CR 134	DAT AIWA HDS1000
Microphone	B&K 4053 (Omni)	SONY ECM307 (Stereo)	Uher M517	B&K 4053 (Omni)
Distance (cm)	40 and 200-300	15-20	?	20 and 250-300
Specimen	released	AA 9945 ROM 40105	Unvouchered	Holotype MNHN 1999.8331
SVL	16	22.7	?	22.5
T°C	25.5	25.5	19	25