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Description of two new species of *Rhinella* (Anura: Bufonidae) from the lowlands of the Guiana shield

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Abstract

The *Rhinella margaritifera* complex is characterisized by the presence of many cryptic species throughout its wide distribution, ranging from Panama to Bolivia and almost entire Amazonia. French Guiana has long been thought to harbor two species of this group (*Rhinella margaritifera* and one unnamed species), though a recent survey using molecular data indicated as many as five lineages. At least three of these lineages do not appear to interbreed despite broad sympatry and thus could be easily regarded as distinct species according to both the biological and phylogenetic species concepts. We examined morphological variation of four of these lineages, along with acoustic data to determine whether these characters discriminate these goups. These analyses, combined with published data of other *Rhinella* species, indicated that two of these lineages represent previously unnamed species. Two of the remainings are allocable to *R. margaritifera* while the status of the fifth is still unclear because so far it is morphologically indistinguishable from *R. castaneotica*.

Key words: Systematics, discriminant analysis, morphology, vocalisation, *Rhinella martyi* sp. nov., *Rhinella lescurei* sp. nov.

Introduction

The *Rhinella margaritifera* complex is a group of bufonid toads supported by two morphological characters (Vélez-Rodriguez 2004), the depressor mandibulae muscle formed by two slips (the first originating on the posterior region of the otic ramus of the squamosal, and the second originating on the anterior region of the otic ramus of the squamosal and the annulus tympanicus), and the presence of a thickening on the ventrolateral border of the quadratojugal that can be seen as a process on the extreme forms. Frost *et al*. (2006) proposed to resurrect the name *Rhinella* (Fitzinger 1826) to group the species of this clade, previously referred to as *Bufo margaritifer* complex or group. In that study *Rhinella margaritifera* was found to be closer to the genus *Rhamphophryne* than any other group of the Bufonidae. This clade includes 12 species: *R. acutirostris* (Spix), *R. alata* (Thominot), *R. castaneotica* (Caldwell), *R. dapsilis* (Myers & Carvalho), *R. hoogmoedi* (Caramaschi & Pombal), *R. magnussoni* (Lima, Menin & de Araùjo), *R. margaritifera* (Laurenti), *R. sclerocephala* (Mijares-Urrutia & Arends), *R. roqueana* (Melin), and numerous undescribed species, across its distribution, from Panama to northern Bolivia. *Rhinella stanlaii* (Lötters & Köhler), *R. proboscidea* (Spix)

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(see Hoogmoed 1986) and *R. scitula* (Caramaschi & De Niemeyer) are tentatively included in this group until additional material is available for study. *Rhinella cristinae* (Vélez-Rodriguez & Ruiz-Carranza), *R. sternosignata* (Günther), *R. intermedia* (Günther), *R. iserni* (Jiménez de le Espada) and *R. ceratophrys* (Boulenger) are excluded from the this group because they do not possess the proposed synapomorphies (above). The position of *Rhaebo nasicus* (Werner, 1903) in Pramuk (2006) also suggestes this species to not belong to this group. Describing new species in this clade is challenging due to the cryptic morphological diversity in the group (similarity between the males, the lack of diagnostic characteristics for females) and the confusion surrounding the names of most of the species due to the poor quality of the type material and some descriptions.

Two species of the *R. margaritifera* complex are known to occur in French Guiana (Lescure & Marty 2000). One is considered by several authors (Lescure & Marty 2000; Vélez-Rodriguez 2004; Hoogmoed 1990, Hoogmoed & Avila-Pires 1991) to represent *R. margaritifera* sensu stricto in which females develop hypertrophied supratympanic crests. The other is not assigned to any known species, is smaller than *R. margaritifera*, and lacks the well developed cephalic crest (Hoogmoed & Avila-Pires 1991; Lescure & Marty 2000). Recently, Haas (2004) suggested that there are actually three species of the *R. margaritifera* complex in northern French Guiana: *R. margaritifera* and two undescribed species.

During surveys in French Guiana, Suriname and Guyana, toads of the *R. margaritifera* complex were sampled from numerous localities (Fig. 1) including vocalization recordings. A previous study using molecular data (Fouquet *et al*. 2007) revealed that five lineages (coded A to E) are present in the eastern Guianas and that at least three lineages likely represent largely sympatric species that are reproductively isolated (Fig. 1). There is no evidence for the reproductive isolation of lineages A+B and C but the A+B lineage appears to be allopatric to lineage C while genetic data suggest incomplete lineage sorting of nuclear DNA. The two well known species (A and E) are widely distributed in French Guiana. Among the additional lineages, one (C) is present in the extreme south of French Guiana, Suriname and Guyana (Fouquet *et al*. 2007; authors' unpubl. data), one (B) is only known from a single localty in the extreme north of French Guiana and species (D) is present in central and southwestern French Guiana. Fouquet *et al*. (2007) noted that lineage D is morphologically more similar to E, as it does not have a developed cephalic crest, though it shares a more recent common ancestor with A, B and C than with E.

Following Vélez-Rodriguez (2005) and Hoogmoed (1977, 1986), we have considered that *Rhinella margaritifera* (=clade A) corresponds to the Guianan populations of *Rhinella* with hypertrophied cranial crests. According to these authors this seems a reasonable conjecture given that the type locality of the species initially called *Rana margaritifera* is Brazil, a country where more than one species with this morphological characteristic occurs. However, more than one species also occurs within the Guianas. Thus, we considered the species occuring in French Guianan with the most hypertrophied cephalic crests as *Rhinella margaritifera* sensu stricto and used *R. margaritifera* (= clade A) specimens to compare with specimens of undescribed species.

We compared specimens and vocalizations from four of the Guianan lineages (excluding B) described in Fouquet *et al*. (2007) and published data of other *Rhinella* species, to determine whether morphological characters are sufficient to discriminate these species. We use these characters to describe two new species and describe their vocalizations and basic ecological characteristics.

Materials and Methods

Measurements of the specimens (lineage A n = 27; C n = 7; D n = 9; E n = 23) were recorded to the nearest 0.1 mm with dial calipers. Sex was determined by observation of the gonads when it was not obvious by sexual dimorphism or calling activity. Measurements follow Vélez-Rodriguez and Ruiz-Carranza (2002) (Snout Vent Length (SVL), Eye Snout Distance (ESD), Femur Length (FML), Foot Length (FTL), Head Length (HL),

Head Width (HW), Tibia Length (TIBL)) except that the paratoid glands were not measured, and that we additionally measured IND (inter nostril distance), UEW (upper eyelid width), IOD (inter orbital distance), EN (eye to nostril distance), ED (eye diameter), ETD (eye tympanum distance), FL1 (first finger length, from distal edge of thenar tubercule to tip of the finger), FL3 (third finger length, from distal edge of thenar tubercule to tip of the finger), TL4 (fourth toe length, from distal edge of metatarsian tubercule to tip of the toe), TD (typanum diameter vertically) and ML (mouth length, from angle of the jaw to the junction of the two mandibules).

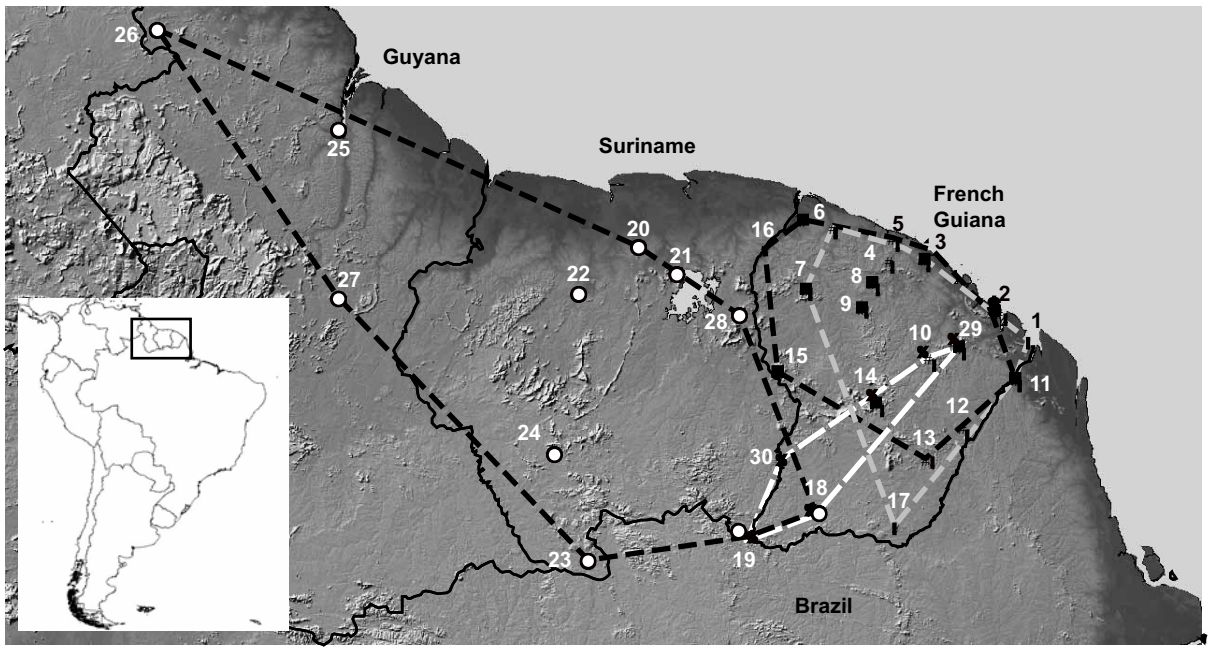

FIGURE 1: Map of sampled areas adapted from Fouquet *et al.* (2007) and additional unpublished data. Black circles: *Rhinella margaritifera* (clade A), white star: *R. margaritifera* (clade B), white circles: *R. martyi* (clade C), white triangles: *R. lescurei* (clade D), white squares: *Rhinella* sp. (clade E).
1 = Ouanary; 2 = Kaw; 3=Guatemala; 4 = Petit-Saut; 5 = Montagne tortue; 6 = St Laurent du Maroni; 7 = Lucifer; 8 = St Elie; 9 = Trinité; 10 = Nouragues; 11 = St Goerges; 12 = Camopi; 13 = Mont Bakra; 14 = Saül; 15 = Montagne Kotika; 16 = Grand Santi; 17 = Trois Sauts; 18 = Haute Wanapi; 19 = Mitaraka; 20 = Goliathberg; 21 = Brownsberg; 22 = Ralleighvallen; 23 = Sipaliwini; 24 = Ellerts de Haan (Kayser); 25 = Bartica; 26 = Baramita; 27 = Kurupukari, 28 = Lely Mountains; 29 = Cisame; 30 = Litany.

All measurements were collected and standardized by dividing through SVL (snout-vent length). We analysed the data using discriminant analyses (XLSTAT-Pro 6.1 for Windows) to identify the key discriminant measures and correlated these with genetic grouping (lineages) and sex groupings.

Specimens collected in French Guiana and Suriname that have been measured were deposited to the Museum National d'Histoire Naturelle de Paris (MNHN). Additional specimens were examined from the Universite Montpellier-2 collection, the Collection of Vertebrates of the University of Texas at Arlington (UTACV), from the Royal Ontario Museum (ROM) and from Brigham Young University (BPN). We used diagnoses and morphological descriptions from Caldwell (1991), Caramaschi and De Niemeyer (2003), Caramaschi and Pombal (2006), Haas (2004), Hoogmoed (1977, 1986, 1990), Hoogmoed and Avila-Pires (1991) Lescure and Marty (2000), Lima *et al*. (in press), Lötters and Köhler (2000), Melin (1941), Mijares-Urrutia and Arends (2001), Myers and Carvalho (1945), Vélez-Rodriguez and Ruiz-Carranza (2002), Vélez-Rodriguez (2004) and Zimmerman and Bogart (1988). We also used description of acoustic signals from Duellman (2005), Lescure and Marty (2000), Marty and Gaucher (2000), Köhler *et al*. (1997), Lima *et al*. (in press) and Zimmerman and Bogart (1988).

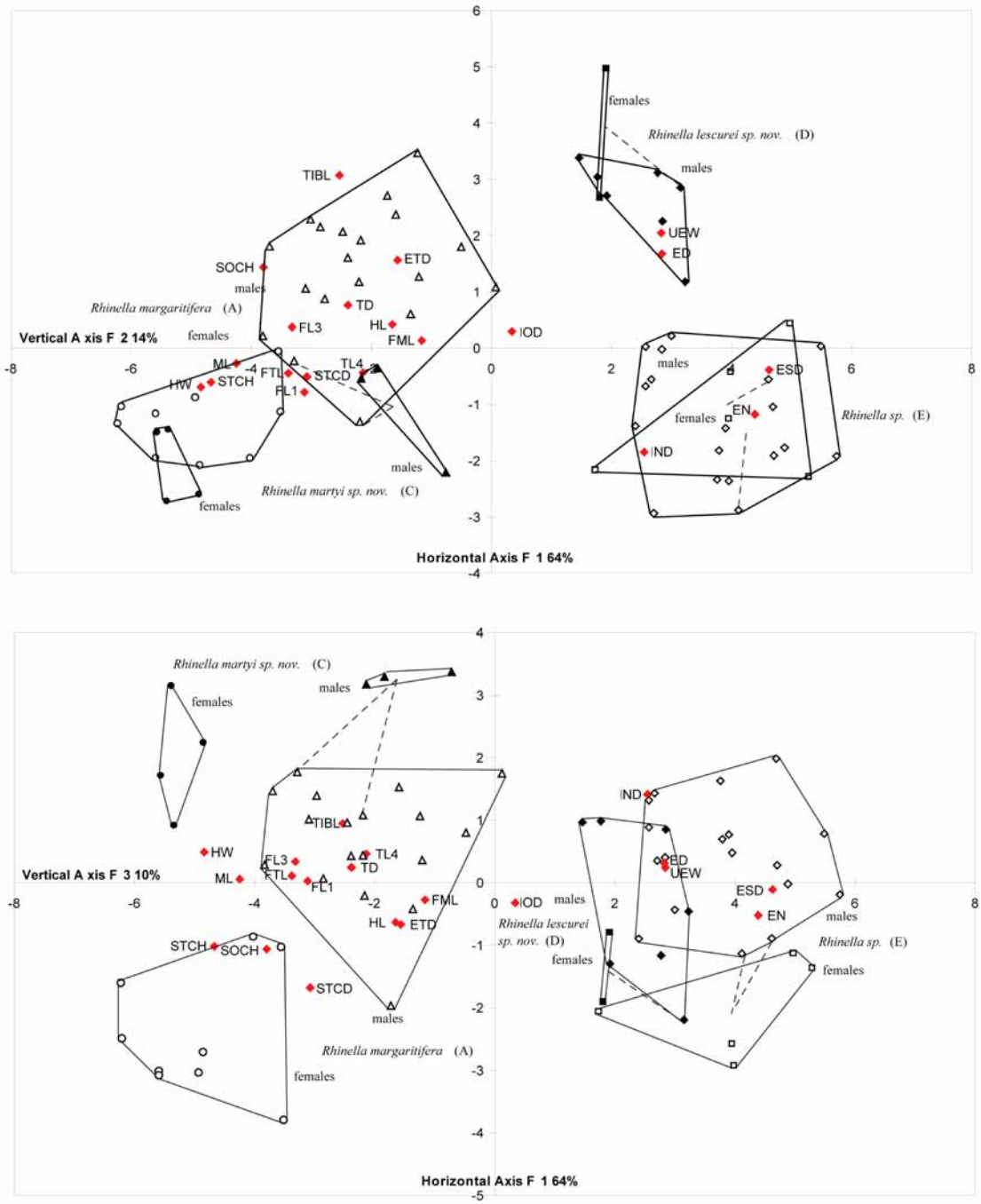

FIGURE 2: Graphical representations along three axis of discriminant analysis on morphological measurements taken from the Guianan *Rhinella margaritifera* species group. Variables in red squares and dashed lines indicate individuals that switched groups.

Recordings were obtained between 2000 and 2006 in French Guiana and Suriname by AF, Christian Marty and PG. Recording equipment included a Marantz PMD670 solid state recorder (Sampling frequency 44.1 kHz) with a built-in XLR microphone, a Sony MZ-NH 700 (minidisc, Hi-MD) (Sampling frequency 44.1 kHz) with a gunzoom MZ00X microphone or a Sony DAT TCD-D8 (Sampling frequency 48 kHz) with a Sennheiser K6 microphone. Distance between recording position and calling individuals varied from about 1 to 2 meters. Settings of the recording level were done manually. No noise reduction systems were used. Tempera-

ture during recording was between 25-26°C. Two calls of two individuals per species (except for lineage D where only one individual was used) were digitized using Raven 1.2.1 (Charif *et al*. 2004) at a sample rate of 44.1 kHz with 16-bit. For spectrogram analyses settings were a filter bandwidth of 1.5 kHz, Fast Fourier Transforms with window size = 1024 points and a frequency of 47 Hz, resolution of 0.1 ms (overlap = 97 %) with Hanning window function.

Results

Using morphology and morphometry, four groups could be confirmed. They largely correspond with material allocated to clades A-E by Fouquet *et al*. (2007). Limited instances of molecular/morphological identification mismatch were observed. Two males of *R. margaritifera* (= clade A) were assigned to *R.* sp. C based on morphological data (Fig. 2), and discrimination among sexes within *R.* sp. E and *R.* sp. D was not strong.

The first axis (Fig. 2) holds 64% of the information and discriminates strongly *R. margaritifera* (= clade A) + *R.* sp. C and *R.* sp. D + *R.* sp. E. Males and females of *R. margaritifera* (= clade A) and *R.* sp. C are also clearly segregated. The variables that mainly contribute to this axis are: ESD, EN, HW, STCH, ML, ED.

The second axis holds 14% of the information and discriminates *R.* sp. D and *R.* sp. E. Males and females of *R. margaritifera* are also clearly segregated along this axis.

The variables that are mainly contributing to this axis are: TIBL, IND, UEW, EN, ED and SOCH.

The third axis holds 10% of the information and discriminates *R. margaritifera* (A) and *R.* sp. C as well as sexes within *R. margaritifera* (A). The variables that mainly contribute to this axis are: STCD, SOCH, STCH and IND.

Our analysis further confirmed that two lineages represent previously unnamed species, corresponding with clades C and D of Fouquet *et al*. (2007). They are described as new species in the following.

Previous authors refered to *R.* sp. E as *Bufo* sp. "*typhonius*" (Lescure and Marty 2000) and *Bufo* sp. 2 (Haas 2004), lacking cephalic crests and referred to as a basal clade by Fouquet *et al*. (2007). No morphological differences obviously distinguish it from *R. castaneotica* from central Amazonia (Caldwell 1991) and the Andean foreland region of Amazonia. Awaiting further revisionary action, we here treat it as *Rhinella* sp. E.

Rhinella martyi sp. nov.

Holotype. MNHN 2006.2601, an adult female (Fig. 3), collected 14 January 2006 by Antoine Fouquet and Christian Marty from Brownsberg Nature Park, Suriname, Brokopondo district (4°56'N/55°10'W), 510 m above sea level (see Fig. 1: 21).

Paratypes. MNHN 2006.2602, MNHN 2006.2603, MNHN 2006.2605, three females collected in the same time and place. MNHN 2006.2604, a male collected in the same time and place. MNHN 2006.2606, MNHN 2006.2607, collected 10 January 2006 by Antoine Fouquet and Michel Blanc nearby the road to Apura and Goliathberg, Para district, Suriname (5°11'N/55°37'W, 50 m above sea level); UTACV 55742-3, collected 20 and 21 December 2002 by Brice Noonan near the Ellerts de Haan airstrip, Sipaliwini district, Suriname (3°6'N/56°28'W); UTACV 55740-1 collected 13 December 2002 by Brice Noonan at Ralleighvallen, Sipaliwini district, Suriname (4°43'N/56°13'W); BPN 897-904, collected 19 May 2003 by Brice Noonan nearby the road to Apura and Goliathberg, Para district, Suriname (5°11'N/55°39'W); BPN 984, 990-91, collected 26 and 30 May 2003 by Brice Noonan near the Sipaliwini village, Sipaliwini district, Suriname (2°2'N/56°7'W); BPN 1053, 1062, collected 3 and 4 June 2003.by Brice Noonan in the Lely Mountains, Suriname, (4°16'N/54°44'W); UTACV 55744 collected 4 January 2002 by Brice Noonan from the type locality; BPN 42, 59 collected 21 and 23 May 1997 by Brice Noonan near Bartica Cuyuni/Mazaruni region, Guyana,

(6°22'N/58°39'W); ROM 20652-20654; collected 11 October 1990 by Ross MacCulloch at Kurupukari, west side of Essequibo River, Potaro-Siparuni District, Guyana (4°40'N/58°39'W, 60 m above sea level); ROM 22813, 22833; collected 24 September and 1 October 1992 by Ross MacCulloch at Baramita, Barima-Waini District (aka Northwest Dist.), Guyana (7°22'N/60°29'W, 100 m above sea level); T3022 (Universite Montpellier-2) collected 10 March 2001 by Philippe Gaucher at Mitaraka, French Guiana (02°16'N/ 54°31'W).

Diagnosis. A large species of the *R. margaritifera* group as defined genetically by Fouquet *et al*. (2007) and morphologically by Hoogmoed (1990) and Vélez-Rodriguez (2004). It is distinguished from all other species of this complex by the following combination of characters (Fig. 3): (1) SVL of 4 females 64.7 ± 3.4mm, of three males 55.3 ± 5.8mm; (2) protruding bony knob at the angle of jaws; (3) *canthus rostralis* with a crest, concave laterally; (4) heel just reaches posterior margin of eye when hindlimbs adpressed; (5) cephalic crests hypertrophied in females and postorbital crests laterally extending very distinct in males; (6) neural spines protruding in females, distinct in males; (7) tympanum large round or ovoid but smaller than eye diameter; (8) parotoid glands relatively small, triangular, posteriorly elongated; (9) upper eyelid without projections; (10) toes about three-quarters webbed, three phalanges free on toe 4; (11) tarsal fold absent; (12) skin tuberculate on dorsal and dorsolateral surfaces, more spinous on limbs; (13) oblique row of tubercles extending from posterior end of postorbital crest to groin; (14) snout pointed dorsally and acute latterally with small fleshy ridge going from tip of snout to the upper lip; (15) iris golden with black reticulations.

Rhinella martyi is distinguished from *R.* sp. E, *R. castaneotica*, *R. magnussoni*, *R. proboscidea*, *R. dapsilis, R. scitula* and the other new species described below by larger SVL and the presence of prominent cephalic crests (Fig. 3). From *R. stanlaii* it differs by larger SVL, the presence of vertebral apophyses salient on dorsum in females and the absence of dermal projection on the eyelid. From *R. hoogmoedi*, the new species is distinguishable by the presence of vertebral apophyses salient on dorsum and by its slightly larger size. From *R. margaritifera* and *R. alata*, it differs by having a more developed bony knob at the angle of the jaw and the shape of its cephalic crests in females: supratympanic and supraorbital crests less high and distance beween supratympanic crests smaller than in *R. margaritifera*. *Rhinella martyi* is larger in SVL and has a proportionately wider and longer head than *R. margaritifera* (Table 1). *Rhinella martyi* can be discriminated from *R. acutirostris* by its angular corner of the jaws and well-developed cephalic crests and from *R. sclerocephala* by neural spines being prominent in females only and the presence of postorbital crests. From *R. roqueana, R. martyi* is distinguished by its smaller size and that the heel does not extend beyond the eye when hind limb carried forward along body.

Description of Holotype (Fig. 3). SVL 66.5 mm; HW 28.0 mm at angle of the jaws; head wider than long, HL 22.0 mm. In dorsal view, snout protruding and rounded laterally, a small, thin vertical fleshy ridge extends from tip of snout to mouth; canthus rostralis concave with crests; top of head flat; cephalic crests well developed; parotoids small, well developed, elongated posteriously; eyelids thick, wide, densely tuberculate; nares slightly protuberant, directed dorsolaterally; corner of mouth with a protruding bony knob; tympanum ovoid, clearly visible. Skin of dorsum and limbs covered with flat tubercules, more numerous and pronounced on limbs, flanks and sides of head, sides with lateral row of large pointed tubercules. Forelimbs slender, relatively long, digits long; tips of digits bulbous; lengths of fingers 4<2<1<3; rudimentary webbing; edges of webbing slighlty tuberculated; thenar (metacarpal) tubercule round, subarticular and supernumerary tubercules present and presence of two tubercules on the second articulation of the finger 3. Hindlimbs slender, inner metatarsal tubercule oval, approximately two times as large as outer; plantar surface with conical subarticular and many supernumerary tubercules. Length of toes 1<2<5<3<4, with well developed webbing; edges of webbing with numerous sipuculous tubercules.

Coloration: dorsum gray-brown with dark brown small patches; dark brown marks also on legs, tarsa and toes; belly cream slighlty orange with more and more small grey spots going to the flanks; throat light grey; interior suface of the tarsa and feet dark brown (except the webbing); no middorsal stripe.

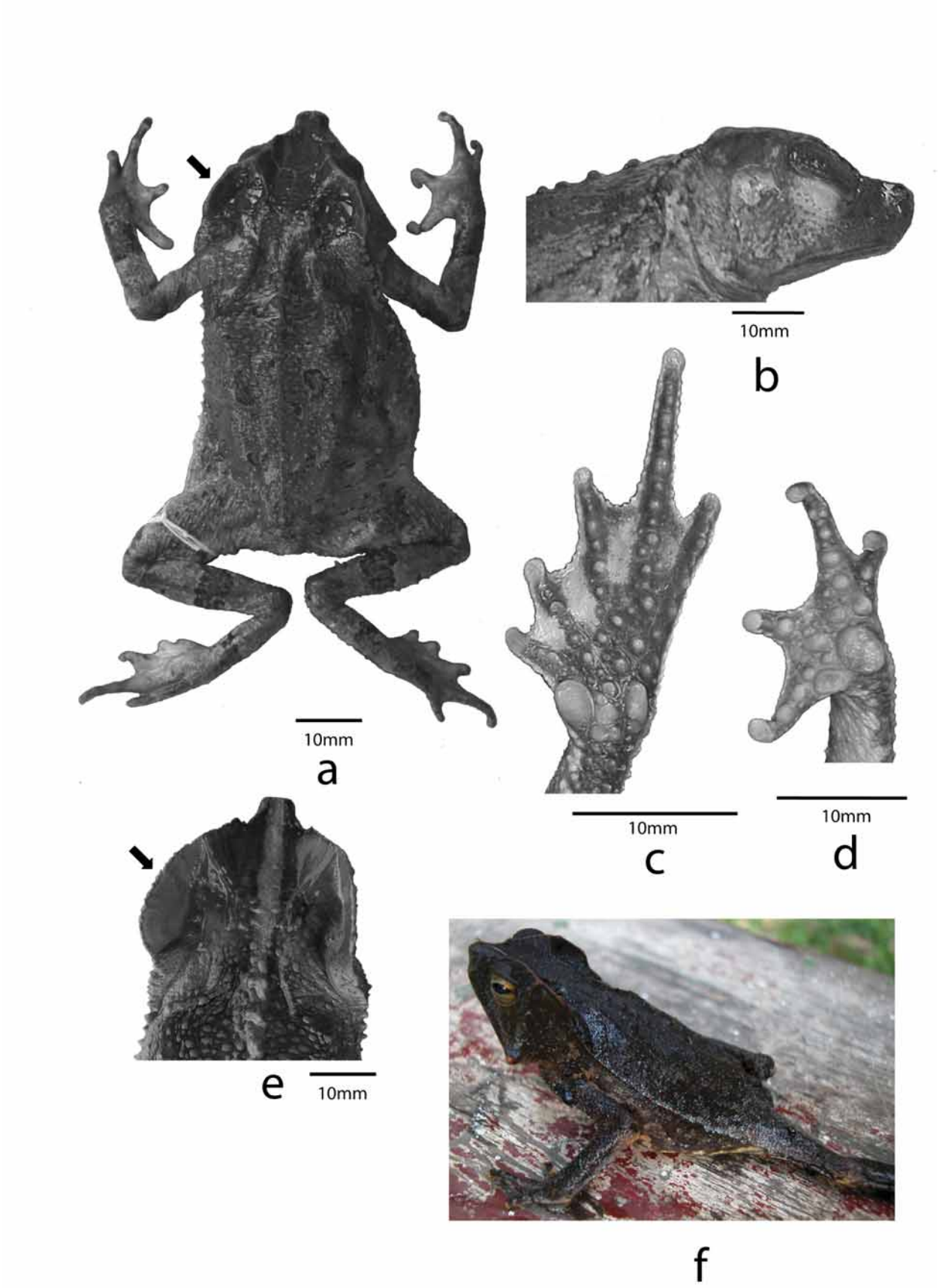

FIGURE 3 A-F: Holotype of *R. martyi* (MNHN 2006.2601): a. dorsal view, b. profile of head, c. ventral view of left foot, d. ventral view of left hand; e: *Rhinella margaritifera* (clade A) (138bm), female, in dorsal view, f. living specimen MNHN 2006.2602. Arrows indicate one of the main character to differenciate the two species.

Variation. This species is highly polymorphic. The coloration of the back varies from dark brown to light gray and sometimes even reddish (Fig. 3 a,f). The patterns are also very variable with a variety of leaf like patterns with successive shades of dark to light brown or gray. A whitish middorsal stripe can occur and can be very thin to 5 mm wide.

Vocalization. The advertisement calls are 295 ms long and composed of approximately 6 groups of pulses on average (Table 2, Fig. 4). These pulses are usually in pairs except the last pulse group that comprises more pulses (up to six). The frequency (mean=1.17 kHz) increases during the call while the time between pulse groups decreases.

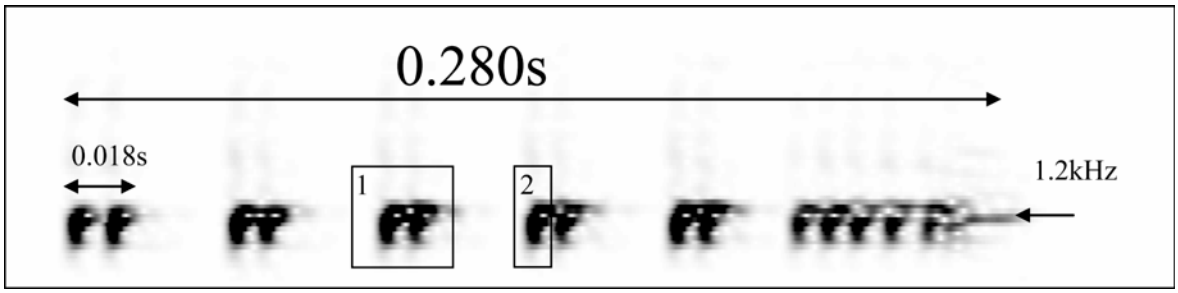

FIGURE 4: *Rhinella martyi* vocalization (one call): (1) pulse-group; (2) pulse.

Distribution and Ecology. This species occurs in most of Suriname including Brownsberg Nature Park, Goliathberg area, Lely mountains, Kaysergebergte, Sipaliwini and Raleighvallen; in southern French Guiana in "Savane layon ouest - Haute Wanapi" and "Sud-Mitaraka", and it is known from Guyana, i.e. Bartica, Kurupukari and Baramita. This species is probably also present in adjacent areas of Brazil and may extend into northeastern Venezuela. No difference in habitat or reproductive behaviour between this species and *R. margaritifera* have been noticed but we know very little about their respective ecologies. This species was observed calling at dawn and during the night in small groups on the road leading to the camp of Brownberg Nature Park after heavy rainfall in January 2006.

Etymology. The name of the species honors the herpetologist Christian Marty who has study the herpetofauna of French Guina for decades providing a geat contribution to our current knowledge.

***Rhinella lescuri* sp. nov.**

Holotype. MNHN 2006.2608, an adult male collected 16 April 2004 by Philippe Gaucher from "Saut wanapi", Haute Wanapi, French Guiana (02°30'694"N/53°494'153"W), 170m above sea level (see Fig. 1: 18).

Paratypes. MNHN 2006.2609, MNHN 2006.2610, MNHN 2006.2612, MNHN 2006.2613, four males collected in the same time and place. MNHN 2006.2611, a female collected by Corine Sarthou at "layon savane Ouest", a very close site from the above one.

PG 103, PG 104, (Philippe Gaucher personal collection) two males collected 12 December, 2002 by Philippe Gaucher from "Crique Limonade", Saül, French Guiana (03º37’N/53º12’W, 100 m above sea level). T3027 (Universite Montpellier-2), collected 10 March, 2001 by Philippe Gaucher from "Mitaraka-Sud", French Guiana (02°16'N/54°31'W, 170 m above sea level). 112BM (Michel Blanc personal collection), a male collected by Michel Blanc from "Litany", French Guiana (02°26'195"N/54°25'184"W, 30 m above sea level). 121BM (Michel Blanc personal collection), a male collected by Michel Blanc from Saül, French Guiana (03º37’N/53º12’W, 100 m above sea level). 5MC, 5'MC (Christian Marty personal collection) a female and a male collected in amplexus by Christian Marty from "camp sisam", French Guiana (04°11'N/52°22'W, 100 m above sea level).

Diagnosis. A medium sized species of the *R. margaritifera* species group as defined genetically by Fouquet *et al*. (2007) and morphologically by Hoogmoed (1990) and Vélez-Rodriguez (2004). It is distinguished from all other species of this complex by the following combination of characters (Fig. 5): (1) SVL of two females 43.7 ± 0.8 mm, of eight males 34.6 ± 4.3 mm; (2) bony knob at angle of jaws absent, corner of mouth angular; (3) *canthus rostralis* smooth, concave laterally, without crests; (4) heel not reaching posterior margin of eye when hindlimbs adpressed; (5) cephalic crests low; (6) neural spines indistinct; (7) tympanum large but smaller than eye diameter, round in males, ovoid in females; (8) paratoid glands relatively small, elongated posteriorly; (9) upper eyelid without projections; (10) toes about three-quarters webbed, three phalanges free on toe 4; (11) tarsal fold absent; (12) skin densely tuberculate, particularly on limbs, less between eyes and center of back in females; tubercules conical with small keratinized spicules; (13) oblique row of tubercules present from posterior corner of pratoid glands to groin; (14) snout pointed with fleshy soft ridge extending to tip of snout; (15) iris golden.

Rhinella lescurei can be distinguished from *R. margaritifera* (A), *R. hoogmoedi*, *R. martyi* (C), *R. stanlaii*, *R. sclerocephala*, *R. roqueana; R. alata* and all the unnamed *Rhinella* species from Colombia identified by Vélez-Rodriguez (2004) by its smaller SVL, the absence of prominent cranial crests, and the very pointed snout due to the presence of a distinct fleshy ridge (Table 1 and see Fig. 5). It can be distinguished from *R. proboscidea* (after Hoogmoed 1986) by its smaller SVL, densely tuberculate skin (smooth skin in *R. proboscidea* although see Zimmerman & Bogart, 1988) and distinct paratoids (indistinct in *R. proboscidea*). *Rhinella lescurei* can be distinguished from *R. dapsilis*, by its tuberculate skin and smaller size and from *R. acutirostris* by its smaller SVL, more pointed snout, angular corner of the jaws, and its small supratympanic ridges (in males and females). From *Rhinella scitula*, it can be mostly distinguished by the poorly distinct cephalic crests, a more pointed snout, and less distinct paratoids. From *R.* sp. E (in sympatry in French Guiana and with which it can be easily confused) and *R. castaneotica*, it can be distinguished by its larger size, the color of the iris (golden vs blue to green in *R.* sp. E and greenish yellow in *R. castaneotica*), the presence of a fleshy ridge at the tip of the snout, larger eyelids (UEW), longer tibia (TIBL), by having its nostrils closer to each other (IND), by having a clearly distinct tympanum, the presence of a lateral row of tubercules, and the outer metatarsal tubercule only two times smaller than the inner one (three times in *R. sp.* (E) and *R. castaneotica*). *R. lescurei* is distinguishable from *R. magnussoni* by its slightly smaller size and by the tuberculated margins of the external part of the feet and the toes.

Description of holotype. MNHN 2006.2608 (Fig. 5). SVL 38.3 mm; HW 14.6 mm at angle of jaws; head shorter than wide, HL 12.8 mm. In dorsal view, snout acuminate, protruding and rounded in lateral view, with pointed vertical fleshy ridge from tip of snout to mouth; canthus rostralis strongly concave, smooth, without crests; top of head flat; cephalic crests poorly developed; paratoid poorly developed, elongated posteriously; eyelid thick, wide, densely tuberculate; nares slightly protuberant, directed dorsolaterally; corner of mouth very angular; tympanum clearly visible, ovoid.

Skin of dorsum and limbs covered with high spicules, more numerous on outer edges of limbs, eyelids, and jaws; sides with a lateral row of large tubercules. Forelimbs slender, relatively long, digits long; tips of digits slightly bulbous; lengths of fingers 4<1=2<3; webbing basal; edge of webbing spinulous; thenar (metacarpal) tubercule ovoid, subarticular and supernumerary tubercules present (Fig. 5). Hindlimbs slender, inner metatarsal tubercle ovoid, approximately two times as large as outer; plantar surface with conical subarticular and many supernumerary tubercles. Length of toes 1<2<3<5<4, webbing well developed, edges of webbing very spinulose (Fig. 5).

Coloration: The dorsum has a leaf like pattern with successive shades of dark to light brown (Fig. 5). Dark brown triangular area are present on the head and lighter patches begin occur between the eyes and the middle of the flanks. Another dark brown mark begins at the middle of the flank and ends before the junction with legs; darker marks are also present across suface the limbs and the fingers. A large dorsal cream stripe extends from the tip of the snout to the end of the body. The flanks are dark brown except for a lighter mark under the eye. The throat is black with very smal white dots, and the belly is cream with large black spots.

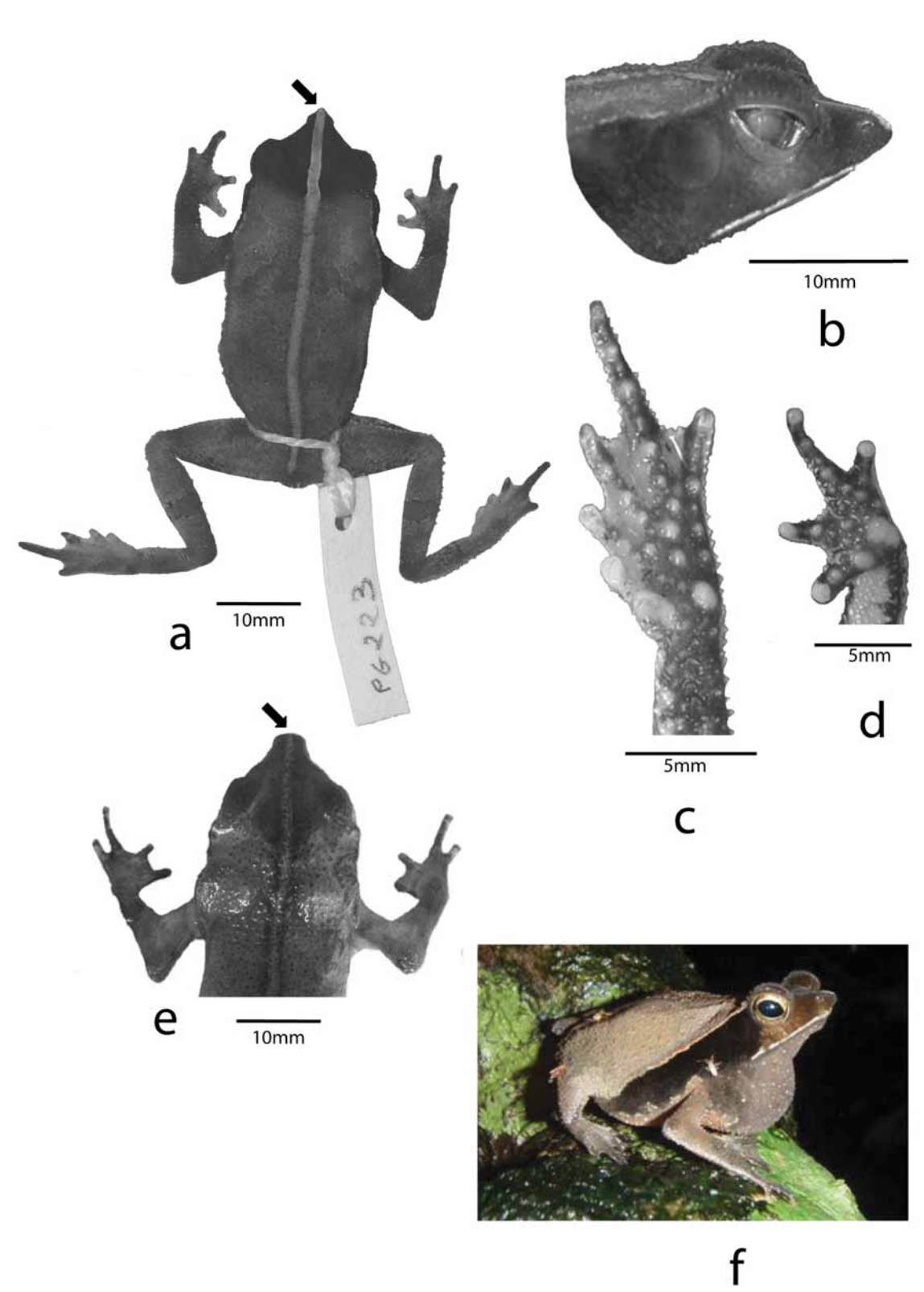

FIGURE 5 A–F: Holotype of *R. lescurei* (MNHN 2006.2608): a. dorsal view, b. profile of head, c. ventral view of left foot, d. ventral view of left hand; e: *Rhinella* sp. E (198bm), male, in dorsal view, f. living specimen, a male calling while perched on a vine. Arrows indicate one of the main character to differenciate the two species.

Variation. This species is also highly polymorphic. The coloration of the back can be uniformly brown to light gray or with a variety of leaf-like patterns (Fig. 3 a,f) with successive shades of dark to light brown or gray. A whitish mid-dorsal stripe can occur and can be very thin to 5 mm wide. Flanks are generally darker than the back.

Vocalization. The calls are long (several seconds) and composed of very short pulse groups that last for 30 ms (Fig. 6, Table 2). Pulse groups are spaced out by 97.2 ms and comprise 4.8 pulses / group on average. The peak frequency is 1.16 kHz and the pulses last 3.45 ms on average.

FIGURE 6: *Rhinella lescurei* fragment of vocalization (two pulse-groups). (1) pulse-goup; (2) pulse.

Distribution and Ecology. Rhinella lescurei is only known from French Guiana, i.e. the southwestern (Haute Wanapi and Mitaraka), central (Saül), western (Litany) and northeastern portions (Cisame camp on Approuague river, Pararé station on Aratai river). Localities range from 20 to 170 m above sea level. During the rainy season (from November to January and from March to May), males call during day time within 10 meters of slowly running water. Calling males are usually isolated from each other and perched between 0.3 and 1 m high on a vine, dead trunk or root. Amplexus is axillary.

Rhinella lescurei probably occurs in southeastern Suriname and Brazilian areas adjacent to French Guiana and Suriname. Preliminary results of an analysis of genetic data spanning the distribution of the *R. margaritifera* group suggest that this taxon could be endemic to the Guiana Shield (Fouquet *et al.*, 2007; authors' unpubl. data).

Etymology. The name of the species honors the herpetologist Jean Lescure who has worked in French Guina for decades and is considered the most important founder of French Guianan herpetology.

Discussion

Rhinella martyi

Rhinella margaritifer (A) and *R. martyi* (C) are morphologically and genetically close. However, morphological and genetic differences are clear and congruent (Fig. 2). These are probably sister species originating in allopatry before Pleistocene according to the high genetic distance between the two lineages (Fouquet *et al.* 2007). They are probably in contact in the southern half of French Guiana. A more detailed study using more samples across a greater geographic range range would probably reveal more diagnostic characteristics.

The structure of the vocalizations are only slightly different between *R. margaritifera* (A), *R. martyi* (C), the *R. margaritifera* complex from Bolivia (Köhler *et al*. 1997), the *R. margaritifera* complex from Amazonian Peru (Duellman 2005) and *R.* sp. E (Fig. 4; Table 2). *Rhinella* sp. E can be distiguished by the peak frequency, which is higher (1.4 kHz) than in the three others. The differences between the vocalizations of *R. margaritifera* (= clade A) and *R. martyi* (= clade C) are small and would probably need a much more important sampling to be discriminated. The peak frequency is slightly lower in *R. martyi* (1.17 kHz) than in *R. margaritifera* (= clade A) (1.26 kHz). Bolivian populations referred to the *R. margaritifera* complex displayed longer calls (316 ms, sd = 15), with a lower dominant frequency (1.14 kHz, sd = 0.01) and more pulse groups

per call (7.9, sd = 0.6) than any of the French Guianan lineages. Calls described in Lescure and Marty (2000) and available in Marty and Gaucher (2000) as *B. margaritifer* and *B. typhonius* correspond respectiveley to *R. margaritifera* (= clade A) and *R.* sp. E.

Rhinella lescurei

This species shares morphological characteristics with *R. proboscidea* and *R. magnussoni* with which it probably close relationships. However, there are slight morphological differences and clear acoustic differences with *R. magnussoni* (Lima *et al*. in press) and *R. proboscidea* (Zimmerman & Bogart 1988). Peak frequency in *R. magnussoni* is between 2.14 and 2.26 kHz and between 1.63 and 3.20 kHz in *R. proboscidea* while it is around 1.16 kHz in *R. lescurei*. The structures of the vocalizations are also different because *R. lescurei* produces groups of pulses (Fig. 6) while there is only a simple structure in *R. magnussoni* and a different structure in *R. proboscidea* which produces longer notes (0.12 s). The structure of *R. lescurei* calls is the most peculiar of the four species occurring in French Guiana (Fig. 6, Table 2). The calls are much longer (several seconds) than the three other Guianan lineages and are composed of very short pulse groups that last for 30ms. Pulse groups are more widely spaced (mean 97.2 ms between pulses) and have more pulses per group (mean = 4.8 pulses/group). These pulse groups are more spaced out (mean 97.2 ms) than in the other species. There are also more pulses per pulse group (mean = 4.8 pulses/pulse-group). The peak frequency and duration are much lower than in the other species (duration mean = 3.45 ms).

Rhinella sp E

Phylogeny topology in Fouquet *et al*. (2007) suggests that *R.* sp. E and *R. castaneotica* are different species, *R.* sp. E being the most basal of the group (see also Pramuk (2006), and Vélez-Rodriguez (2004) for *R. castaneotica* phylogenetic position). However, we did not find any obvious character differences between *R.* sp. E and *R. castaneotica* from Parà as described by Caldwell (1991). Moreover, the ecology of *R.* sp. E is also similar to that of *R. castaneotica* except that *R.* sp. E in French Guiana usually uses stalks of dead palm leaves full of water or small holes in dead trunks instead of the fruit capsules of the Brazil nut tree used for breeding by Brazilian populations. We consequently need futher analyses, especially to compare specimens of these two species and different kinds of data (e.g. vocalization, larval morphology, detailed osteology, etc.), to be able to describe this species. This species is also one of the two "undescribed" species in Haas (2004).

Other undescribed species

The other "undescribed" species (sp. 1) from Kaw Mountain (north of French Guiana), according to Haas (2004) is supposedly smaller than *R. margaritifera*, with indistinct paratoids and lacks hypertrophied cranial crests. We assume that Haas (2004) examined small and probably relatively young *R. margaritifera* individuals in which paratoids and cranial crests are not yet fully developed (pers. obs.). However, one lineage (*R. margaritifera* B) appears to be restricted to the Kaw mountain (north of French Guiana) as detailed by Fouquet *et al*. (2007) but we sampled too few individuals of the lineage to add this group to our morphometric analysis. Nevertheless, we did not notice any morphological differences with *R. margaritifera* (A) (e.g. hypertrophied cephalic crests) and the genetic data indicated that *R. margaritifera* A and B are indeed very close and are unlikely to represent different species. Consequently, it is very unlikely that a species morphologically different from *R. margaritifera* is occuring in this region.

Rhinella dapsilis

R. dapsilis appears to be genetically very close to *R. margaritifera* (A) in Fouquet *et al*. (2007) who used a mitochondrial DNA sequence published by Pramuk (2006). Both are closer to each other than to *R. martyi* (C). However, *R. dapsilis* and *R. margaritifera* are supposedly morphologically different (Myers & Carvalho 1945). The main differences are that *R. dapsilis* lacks cranial crests and has smooth skin. Moreover, Pramuk

(2006) used specimen (QCAZ 3509) sampled near Pichincha which is on the pacific side (trans-Andean) of the Andes while *Rhinella dapsilis* is supposed to be distributed on the Amazonian side (Cis-Andean). To fully elucidate the taxonomic relationship between these entities requires additional work, but we can make several hypotheses: (1) *R. dapsilis* and *R. margaritifera* (A) originated relatively recently from a common ancestor and *R. dapilis* secondarily lost prominent cranial crests and rough skin. (2) The *R. dapsilis* sequences from Pramuk (2006) come from a misidentified specimen of a close relative of *R. margaritifera* (A) or even from a cross-contamination. In any case, it is interesting to note that the lineage formed by *R. margaritifera* A+B+*R. dapsilis* from Pramuk (2006) could be present from north French Guiana to the other side of the Andes in Ecuador through the Amazon Basin. The second hypothesis is most likely because we re-examined the *R. dapsilis* specimen that Myers and Carvalho (1945) described (an adult female without any cranial crest and smooth skin) and confirmed that *R. dapsilis* is a valid species. However, we have yet to find another female with similar dimensions and characteristics. Moreover, the males that have been identified as *R. dapsilis* from different collections are associated with females having very high crests suggesting probable misidentification (Vélez-Rodriguez pers. obs.).

Conclusion

When several kind of data converge to similar results, this provide a strong support for independent specific status. Here, even if differences are small between *R. margaritifera* and *R. martyi*, the use of fine analytical tools provide evidence that they belong to different species and help describing them. However, morphometric, acoustic and genetic data are in conflict concerning the relationship between *R. lescurei* and the other lineages occuring in French Guiana. Morphological similarities exist between *R. lescurei* and *R.* sp. E (Fig. 2), particularly the lack of developed cephalic crests. However, it shares a more recent common ancestor with *R. margaritifera* (A) and *R. martyi* (C) than with *R.* sp. E according to genetic data (Fouquet *et al*. 2007) and its vocalizations are considerably different from all other species. Such incongruences are common and underline the cryptic trend in amphibian morphological evolution (Bickford *et al*. 2007) and the relevance of incorporating multiple types of data like acoustic, genetic and morphometric.

The taxonomy of the *R. margaritifera* species remains confusing, but with the help of molecular and ecological data we are confident that it can be resolved in the near future.

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TABLE 1 Morphometric measurements. Abbreviations are explained in the text. Means and standard deviations (sd) are presented my lineages and sexes. From the "/SVL" line the following measurements are divided through SVL (snout-vent length).

	R. margaritifera A				*R. martyi nov. sp .C*				*R. lescurei nov. sp. D*				*R. sp. E*			
	Males (n=18)	sd	Females (n=9)	sd	Males (n=3)	sd	Females (n=4)	sd	Males (n=7)	sd	Females (n=2)	sd	Males (n=18)	sd	Females (n=5)	sd
SVL	**46.91**	5.861	**59.42**	10.115	**52.33**	4.924	**62.85**	3.131	**34.57**	4.359	**43.70**	0.849	**31.04**	2.282	**34.77**	2.835
ESD	5.67	0.783	7.12	1.341	6.93	0.473	7.71	0.397	5.15	0.486	6.00	0.141	4.51	0.341	5.01	0.442
FML	19.34	3.636	24.17	4.059	20.63	2.122	26.53	1.212	14.00	1.587	17.90	0.424	12.39	1.340	14.05	1.411
FTL	11.15	1.810	14.61	2.312	12.50	1.300	15.30	0.560	7.30	0.931	9.65	0.354	6.78	1.037	7.22	1.244
HL	15.80	2.297	20.53	3.796	17.97	1.447	21.93	0.650	11.99	1.308	15.15	0.071	10.25	0.685	11.80	1.059
HW	19.34	3.072	25.41	5.057	22.43	2.214	28.15	0.947	13.24	1.674	15.95	0.212	11.59	1.127	13.00	1.544
TIBL	19.74	2.729	23.51	3.800	21.30	2.252	25.43	0.903	14.07	1.620	18.45	0.636	12.07	1.189	13.00	1.241
IND	2.47	0.391	2.95	0.592	3.17	0.321	3.55	0.238	1.92	0.400	2.05	0.212	1.86	0.222	1.95	0.235
UEW	3.61	0.488	4.00	0.610	4.43	0.551	4.25	0.545	3.37	0.538	3.53	0.530	2.47	0.246	2.91	0.301
IOD	6.86	0.996	8.30	2.050	7.37	0.351	7.70	2.708	4.64	0.492	5.90	0.141	4.36	0.480	5.13	0.428
EN	3.96	0.538	5.12	1.021	4.57	0.231	5.13	0.330	3.24	0.435	4.23	0.106	3.14	0.262	3.57	0.418
ED	6.71	0.758	7.72	1.269	7.30	0.872	8.25	0.265	5.19	0.606	6.30	0.141	4.48	0.398	5.18	0.319
ETD	0.82	0.253	1.13	0.187	0.93	0.351	1.05	0.387	0.69	0.219	0.90	0.424	0.41	0.119	0.60	0.255
FL1	5.27	1.104	7.33	1.475	6.00	0.100	8.63	0.718	3.94	0.508	4.90	0.707	3.07	0.417	3.54	0.373
FL3	12.46	1.875	15.55	2.668	13.60	0.854	16.83	1.001	8.41	1.024	10.93	0.389	7.52	0.858	8.46	1.163
TL4	17.13	2.714	21.31	3.788	19.13	2.055	22.28	0.780	11.50	1.356	14.90	0.566	10.85	1.488	11.80	1.554
TD	3.93	0.602	4.94	1.034	4.33	1.060	4.93	0.465	2.67	0.702	3.15	0.212	2.28	0.384	2.50	0.321
ML	14.20	2.003	18.46	3.314	16.07	1.429	19.93	0.695	9.89	1.090	12.90	0.141	8.80	0.796	10.00	0.836
SOCH	8.83	1.141	11.74	2.173	9.20	1.058	11.50	0.346	6.38	0.794	7.85	0.071	5.27	0.403	6.05	0.517
STCD	17.22	2.380	24.08	4.114	17.70	1.229	23.53	1.578	12.41	1.286	15.68	0.530	11.02	0.928	12.43	1.180
STCH	9.89	1.797	16.08	4.343	9.83	1.002	14.63	1.613	6.03	0.574	7.83	0.460	5.26	0.325	5.94	0.716
/SVL																
ESD	0.12	0.009	0.12	0.010	0.13	0.006	0.12	0.006	0.15	0.007	0.14	0.006	0.15	0.008	0.14	0.006
FML	0.41	0.042	0.41	0.018	0.39	0.008	0.42	0.008	0.41	0.018	0.41	0.018	0.40	0.022	0.40	0.022
FTL	0.24	0.014	0.25	0.037	0.24	0.008	0.24	0.011	0.21	0.006	0.22	0.004	0.22	0.021	0.21	0.020
HL	**0.34**	0.013	**0.34**	0.017	**0.34**	0.008	**0.35**	0.014	0.35	0.008	0.35	0.008	0.33	0.013	0.34	0.008
HW	**0.41**	0.019	**0.43**	0.024	**0.43**	0.007	**0.45**	0.018	0.38	0.010	0.37	0.012	0.37	0.017	0.37	0.017
TIBL	0.42	0.012	0.40	0.007	0.41	0.013	0.40	0.010	**0.41**	0.012	**0.42**	0.006	**0.39**	0.018	**0.37**	0.009
IND	0.05	0.004	0.05	0.006	0.06	0.003	0.06	0.005	0.06	0.006	0.05	0.004	0.06	0.005	0.06	0.003
UEW	0.08	0.010	0.07	0.008	0.08	0.008	0.07	0.008	0.10	0.005	0.08	0.011	0.08	0.009	0.08	0.010
IOD	0.15	0.008	0.14	0.020	0.14	0.007	0.12	0.046	0.13	0.006	0.14	0.001	0.14	0.008	0.15	0.005
EN	0.08	0.006	0.09	0.006	0.09	0.011	0.08	0.006	0.09	0.003	0.10	0.001	0.10	0.008	0.10	0.006
ED	0.14	0.010	0.13	0.008	0.14	0.005	0.13	0.005	0.15	0.004	0.14	0.006	0.14	0.009	0.15	0.013
ETD	0.02	0.005	0.02	0.003	0.02	0.005	0.02	0.006	0.02	0.005	0.02	0.009	0.01	0.004	0.02	0.006
FL1	0.11	0.012	0.12	0.010	0.12	0.010	0.14	0.013	0.10	0.043	0.11	0.014	0.10	0.011	0.10	0.004
FL3	0.27	0.015	0.26	0.016	0.26	0.016	0.27	0.018	0.24	0.006	0.25	0.004	0.24	0.018	0.24	0.022
TL4	0.36	0.019	0.36	0.011	0.37	0.026	0.35	0.012	0.33	0.011	0.34	0.006	0.35	0.028	0.34	0.024
TD	0.08	0.008	0.08	0.009	0.08	0.013	0.08	0.010	0.08	0.014	0.07	0.003	0.07	0.010	0.07	0.011
ML	0.30	0.012	0.31	0.016	0.31	0.002	0.32	0.009	0.29	0.009	0.30	0.009	0.28	0.013	0.29	0.006
SOCH	**0.19**	0.008	**0.20**	0.011	**0.18**	0.009	**0.18**	0.008	0.18	0.005	0.18	0.002	0.17	0.010	0.17	0.008
STCD	**0.37**	0.019	**0.41**	0.025	**0.34**	0.015	**0.37**	0.019	0.36	0.013	0.36	0.019	0.36	0.016	0.36	0.008
STCH	**0.21**	0.017	**0.27**	0.049	**0.19**	0.009	**0.23**	0.023	0.18	0.008	0.18	0.014	0.17	0.008	0.17	0.009

TABLE 2: Acoustic measurements. Means followed by sampling size (n) and standard deviation (sd) are presented.

	R. margaritifera (clade A)	*R. martyi* (clade C)	*R. lescurei* (clade D)	*Rhinella* sp. (clade E)	remarks
calls/minute	69	81	1 to 10	90	too few data for D
	n = 2; sd = 4.24	n =And so on 2; sd = 21.21	/	n = 2; sd = 0	
call duration (ms)	287.975	295.125	30 ms / pulse-group	273	
	n = 4; sd = 45.40	n = 4; sd = 13.09	n = 10; sd = 0	n = 4; sd = 9.69	
peak frequency/ pulse group	1.265	1.169	1.161	1.407	increasing slightly within each call for A,C,E
	n = 27; sd = 0.035	n = 24; sd = 0.04	n = 7; sd = 0.015	n = 24; sd = 0.037	
pulse-groups/call	6,75	6	480 / min	6	
	n = 4; sd = 0.957	n = 4; sd = 0	/	n = 4; sd = 0	
pulses/pulse-group	2 (3.25 last one)	2 (4.75 last one)	4.83	2 (4.5 last one)	last pulse group with more pulses for representatives of clades A,C,E
	n = 23; sd = 0 (n = 4; sd = 0.5)	n = 20; sd = 0 (n = 4; sd = 0.96)	n = 7; sd = 0.787	n = 20; sd = 0 (n = 4; sd = 0.577)	
pulse duration (ms)	8.44	9.55	3.45	8.54	
	n = 24; sd = 0.726	n = 24; sd = 1.179	n = 6; sd = 0.164	n = 24; sd = 1.184	
inter pulse-groups duration (ms)	25.94	25.56	97.2	28.85	decreasing by half within each call for representatives of clades A,C,E
	n = 23; sd = 6.868	n = 20; sd = 3.583	n = 5; sd = 17.754	n = 20; sd = 3.911	

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