

## Redescriptions of Two Toad Species of the Genus *Atelopus* from Coastal Venezuela

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*Atelopus* is a species-rich genus of toads from the Neotropics. Many species of this genus are regarded as vulnerable or endangered because of apparent population declines. In most cases, reasons for declines remain unknown. Conservation efforts are needed, which require a profound knowledge of taxonomy. This paper contributes to the taxonomic status of *Atelopus* populations from the coastal mountain range of Venezuela. *Atelopus cruciger* is redescribed on the basis of the neotype and additional material from nine localities. *Atelopus vogli* here is considered a distinct species (not a junior synonym or subspecies of the former) known only from the type series and a few additional specimens collected at one single locality, which has been severely altered. The latter species lacks (whereas *A. cruciger* has) color pattern on the dorsum and is (in both sexes) smaller than *A. cruciger*. The two taxa also differ in hand morphology and characters of the sphenethmoid. Because of population declines in *A. cruciger* and the absence of recent records of *A. vogli*, in spite of intensive searches for both taxa, they should be considered as critically endangered. Comprehensive investigation evaluating the population status of both species is urgently recommended.

*Atelopus* es un género especioso de sapos del Neotrópico. Muchas especies en este género son consideradas como vulnerables o en peligro de extinción debido a aparentes disminuciones poblacionales. En la mayoría de los casos, las razones para estas disminuciones son desconocidas. Se necesitan esfuerzos de conservación, los cuales requieren de un profundo conocimiento de taxonomía. Este trabajo contribuye con el estatus taxonómico de las poblaciones de *Atelopus* de la Cordillera de la Costa de Venezuela. *Atelopus cruciger* es redescrito sobre la base del neotipo y material adicional de nueve localidades. *Atelopus vogli* es considerado aquí como una especie distinta (no un sinónimo reciente o una subespecie de la anterior) conocida solamente de la serie tipo y unos pocos ejemplares adicionales coleccionados en una localidad única muy perturbada actualmente. Esta última especie carece (mientras que *A. cruciger* tiene) de patrón de coloración dorsal y es (en ambos sexos) más pequeña que *A. cruciger*. Los dos taxa también difieren en la morfología de la mano y caracteres del esfenoides. Debido a las disminuciones poblacionales en *A. cruciger* y la ausencia de registros recientes de *A. vogli*, a pesar de búsquedas intensas para ambos taxa, ellas deben ser consideradas como en peligro crítico. Se recomienda urgentemente una investigación comprehensiva que evalúe el estatus poblacional de ambas especies.

*A*TELOPUS is a species-rich toad genus from the Neotropics. Currently more than 75 species are recognized (Löters, 1996; unpubl. data). Previous investigations (e.g., Coloma et al., 2000) have documented the persistence of several alpha-taxonomic problems within the genus. A deep understanding of taxonomy is the basis for not only phylogenetic investigations (cf. Coloma, 1997) but also the implementation of conservation efforts (Duellman, 1999). The latter is of special importance with respect to the genus *Atelopus*. Throughout Central and South America, many populations of this genus are regarded as “endangered” or “critically endangered” (IUCN, 2001, IUCN Red List Cate-

gories and Criteria: vers. 3.1. IUCN Species Survival Commission; <http://www.iucn.org/themes/ssc/redlists/redlistcatsenglish.pdf>), because populations are known to have declined dramatically (e.g., Pounds and Crump, 1994; La Marca and Löters, 1997; Ron et al., 2003). We here contribute to the taxonomic status of *Atelopus* populations from the coastal mountain range of Venezuela that seem to have undergone drastic population declines (Manzanilla Puppo et al., 1995; Rodríguez and Rojas-Suárez, 1995; La Marca and Löters, 1997).

*Atelopus* populations from the coastal mountain range of Venezuela have commonly been associated with the name *Atelopus cruciger* (Lich-

tenstein and Martens). For a list of references see Lötters (1996:22). However, Lötters et al. (1998) discovered that the type material of *A. cruciger* originated from Central America and actually represents *Atelopus varius* (Lichtenstein and Martens). With the goal to warrant taxonomic stability, Lötters and La Marca (2001) proposed to the International Commission on Zoological Nomenclature (ICZN) to set aside previous type fixations for *A. cruciger* and to designate a neotype from coastal Venezuela. This was accepted (ICZN, 2002).

All material from the Venezuelan coastal mountain range examined by us is referable to *A. cruciger* (as represented by the neotype) on the basis of morphology, morphometrics, and osteology. There is one exception, however. A subspecies has been proposed, *Atelopus cruciger vogli* Müller. Although from the same general area, material of this form is unlike the nominotypical form, mainly by lacking dorsal markings. It was collected in 1933 and again somewhat later at the type locality only (Müller, 1934, 1935; Rivero, 1961). Recent efforts have produced no additional specimens in the area of the type locality of *A. c. vogli* because of anthropogenic landscape change (Manzanilla Puppo et al., 1995). As a result of limited knowledge, publications dealing with *A. c. vogli* are sparse (for list of references, see Lötters, 1996:23), and most continued the subspecific treatment. Because *A. c. vogli* and the widespread *A. c. cruciger* were distinguished mainly by color pattern (Müller, 1934; Rivero, 1961), La Marca and Lötters (1997) concluded that they may be synonymous. Although both names have never been formally synonymized, recent publications dealing with *Atelopus* in Venezuela (e.g., La Marca et al., 1990 ("1989"); La Marca, 1997; Péfaur, 1992) refer to the name *A. cruciger* only (but see Barrio Amorós, 1998). We included the type material of *A. c. vogli* into an analysis of *A. cruciger* from nine different localities. Our conclusion is that the two are distinct taxa. We suggest specific status for *A. c. vogli*. The purpose of this paper is (1) to provide for the first time detailed descriptions of both species including intraspecific variation and (2) to describe parts of the skeletons of both taxa.

#### MATERIALS AND METHODS

We examined 193 specimens (including the neotype) from nine populations of *A. cruciger* and the holotype plus 415 topotypic specimens of *A. vogli*. All material examined is listed in Appendix 1; respective localities are shown in Figure 1. Museum abbreviations follow Leviton et

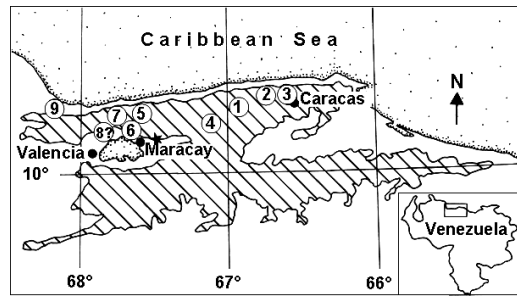


Fig. 1. Map of northern Venezuela showing type locality of *Atelopus vogli* (star) and studied populations of *Atelopus cruciger* (numbers 1–9; number 7 corresponds to locality of the neotype). For locality details, see Appendix 1. Shaded area depicts regions higher than 1000 m above sea level. Insert at lower right corner shows approximate position of the area enlarged within Venezuela.

al. (1985) except FMC (Fundación Museo de Ciencias, Caracas) and ULABG (Universidad de Los Andes, Laboratorio de Biogeografía, Mérida). Sexes of specimens were determined by external features (i.e., broadened forearms and the presence of nuptial excrescence in males, eggs visible through skin of venter in females; see Lötters, 1996) or by dissection. We describe webbing formulae using the system developed by Savage and Heyer (1969, 1997) and modified by Myers and Duellman (1982).

Measurements on adult specimens were made with calipers to the nearest 0.1 mm. For the morphometric analysis, 34 females and 60 males of *A. cruciger* were chosen at random. Morphometric data for *A. vogli* are based on 20 females and 20 males, all chosen at random. Abbreviations of measurements are SVL (snout-vent length), HDWD (head width), HLSQ (head length from the squamosal), EYDM (eye diameter), ITNA (internarial distance), EYNO (eye to nostril distance), SW (sacrum width at widest), TIBL (tibia length), FOOT (foot length), HAND (hand length), THBL (thumb length). Definitions of measurements follow Gray and Cannatella (1985) except SW (cf. Coloma, 1997). A two-factorial analysis of variance (ANOVA) was performed (with the software STATISTICA 5.0, StatSoft, Inc.), testing "sex" and "taxon" with the measurements as response variables.

For osteological examination, four adult females and three adult males of *A. cruciger* (from three localities) and three adult females and five adult males of *A. vogli* were skinned and the viscera removed. Specimens (see Appendix 1) were stained with alizarin red and alcian blue for staining bones and cartilage, respectively,

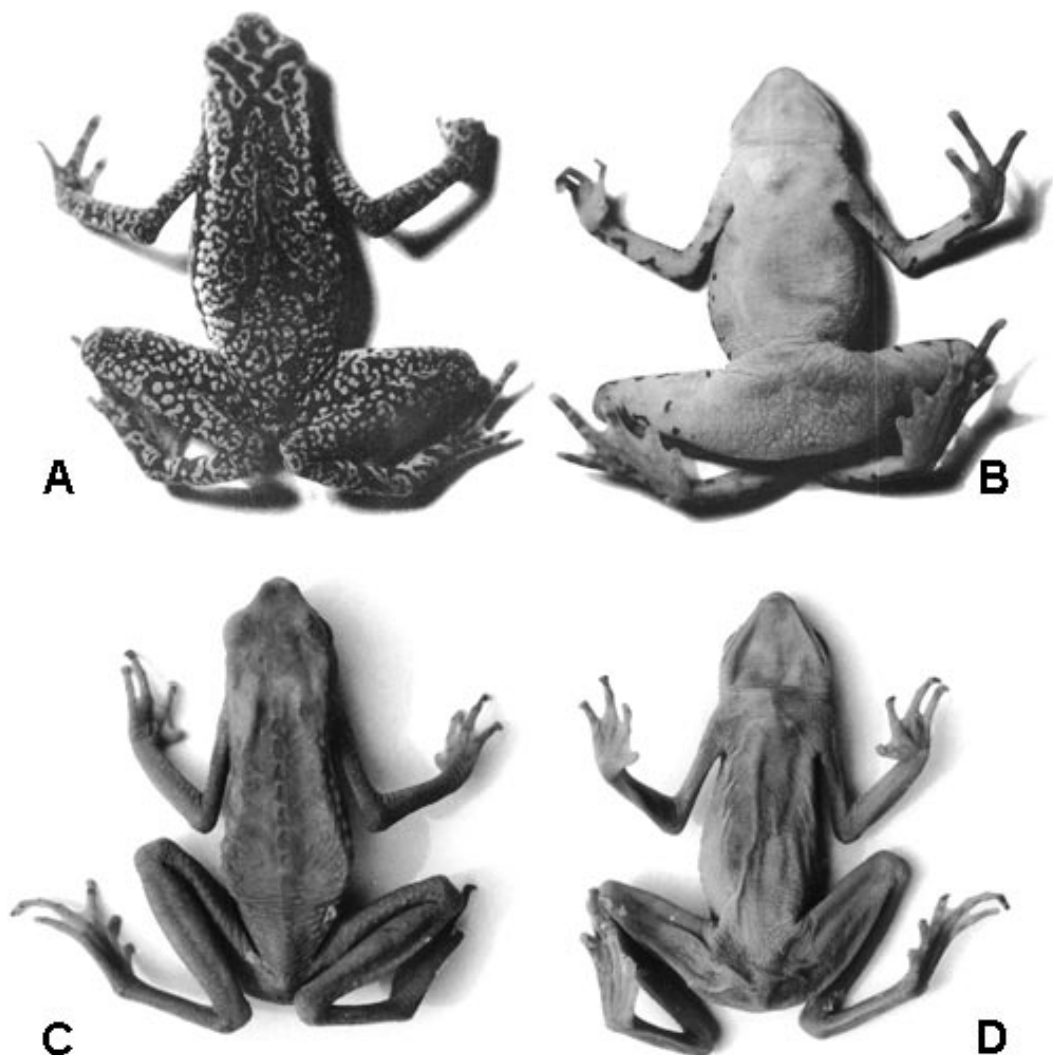


Fig. 2. (A–B) Dorsal and ventral views of neotype of *Atelopus cruciger* (ZSM 93/1947/10), and (C–D) of holotype of *Atelopus vogli* (ZSM 3/1933).

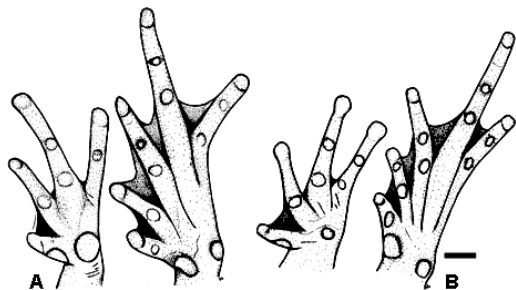


Fig. 3. (A) Sole and palm of neotype of *Atelopus cruciger* (ZSM 93/1947/10), and (B) of holotype of *Atelopus vogli* (ZSM 3/1933). Bar equals 2 mm.

following the method of Dingerkus and Uhler (1977) with modification (Plösch, 1991).

#### SYSTEMATICS

*Atelopus cruciger* (Lichtenstein and Martens)  
Figures 2–3

*Phrynidium crucigerum* Lichtenstein and Martens, 1856:41. Neotype: ZSM 93/1947/10 (Figs. 2–3), an adult female from Parque Nacional Henri Pittier from “the vicinity of Rancho Grande on the road from Maracay to Ocumare de la Costa (approximately 1000 m above sea level), Estado Aragua, Venezuela” (Lötters and La Marca, 2001: 120), approximately at 10°22′01″N, 67°41′01″W.

*Phryniscus bibronii* (non O. Schmidt): Günther, 1859 "1858":137; Boulenger, 1882:155; Boettger, 1893:39.

*Phryniscus cruciger*: Günther, 1859 "1858":44; Boulenger, 1882:154.

*Atelopus (cruciger) cruciger*: Nieden, 1926:84; Lutz, 1927:38; Müller, 1934:151, 1935:2; Rivero, 1961:171, 1964:311; Solano, 1969:21; Harding, 1983:56; La Marca, 1992:13, 1997:113; Frost, 1985:29; Péfaur, 1992:3; Lötters, 1996:22; Barrio Amorós, 1998:5; Lötters and La Marca, 2001:120.

*Atelopus bibronii* (non O. Schmidt): Lutz, 1927:38.

*Atelopus spumarius* (non Boulenger): Lutz, 1927:38.

**Diagnosis.**—An *Atelopus* with (1) SVL of adult females 39.5–49.9 mm ( $n = 34$ ), of adult males 28.2–34.6 mm ( $n = 60$ ); (2) snout pointed in dorsal view; upper jaw, in lateral view, protruding beyond lower; (3) neural spines visible externally; (4) long hind limbs (TIBL/SVL 0.42–0.51,  $n = 94$ ), length of foot more than three-fourths length of tibia (FOOT/TIBL 0.83–0.95 in 34 females, 0.83–0.90 in 60 males); (5) tympanic membrane, tympanic ring, and ostia pharyngea absent; (6) small rounded warts (in part conical; no spiculae) present on dorsolateral and lateral surfaces posterior to eye, continuing in dorsolateral row, on posterior dorsum, and on dorsal surfaces of entire arm and entire leg and partly on hand and tarsus; (7) outer and inner metatarsal and metacarpal tubercles present, remaining plantar and palmar surfaces free of tubercles, or palm with few supernumerary tubercles; distinct subarticular tubercles at joints of most phalanges of all toes and Fingers II–IV; (8) foot webbing formula I0–1–II0–1+III0+ to IIII–2IV2–1–V; hand webbing formula I0–1+III1–2+III2–2IV (basal webbing between Fingers II–III, less or absent between III and IV); (9) thumb about half hand length (THBL/HAND 0.43–0.54,  $n = 96$ ), containing two phalanges; Finger III relatively long (HAND/SVL 0.25–0.28,  $n = 96$ ); tips of Fingers II–IV broadened; (10) in preservative, dorsum yellowish to greenish-tan, ventrally lighter (in life, dorsally yellowish-green to olive, ventrally turning into yellowish-cream, without reddish markings), with a brown or black (as in life) lateral band, and brown or black (as in life) stipples, vermiculation or marbling on all dorsal surfaces as well as a more or less defined cross-pattern behind the head and sometimes a chevron mark in the sacral region.

*Atelopus cruciger* is most similar to *A. vogli* from which it can be distinguished by the presence

of a dark dorsal pattern (absent in *A. vogli*; Fig. 2), larger size (Tables 1–2), size of palmar and thenar tubercles (smaller in *A. vogli*; Fig. 3), and in characters of the sphenethmoid (Fig. 4). There are several other "warty" *Atelopus* taxa from the northern and central Andes of South America exhibiting greenish color with dark pattern (cf. Lötters, 1996). *Atelopus cruciger* can be distinguished from all by the presence of warts on the entire arm and leg, having basal hand webbing, and from many by absence of white or yellowish warts or spots and/or absence of spiculae and/or presence of two thumb phalanges.

Coloma (1997) suggested that the poorly known *Atelopus pedimarmoratus* Rivero from the Cordillera Oriental of Colombia probably was related to *A. cruciger*. *Atelopus pedimarmoratus* can be distinguished from *A. cruciger* by having fewer warts (including arm, leg, and flank), diffuse yellow spots, and the absence of basal hand webbing (cf. Rivero, 1963a; Lynch, 1993).

**Description of neotype.**—Body slender; neural spines visible externally; head longer than broad; head length less than one third SVL; snout pointed in dorsal view, with tip rounded, slightly depressed; in lateral aspect, upper jaw protruding beyond lower; nostril lateral, weakly protuberant and hardly visible from above; tongue more than three times longer than wide, broadest posteriorly, free for two-fifths of its length posteriorly; choanae small, rounded; ostia pharyngea absent; canthus rostralis straight from nostril to tip of snout, barely concave and longer from nostril to anterior corner of eye; eye width longer than distance from nostril to anterior corner of eye; loreal area barely concave; upper lip not fleshy; temporal area straight; tympanic membrane and tympanic ring absent; dorsolateral postorbital (supratympanic) crest well developed, somewhat shorter than eye width. Tibia long, less than half SVL; foot shorter than tibia; metatarsal tubercles distinct, outer rounded, inner ovoid, about twice the size of outer; rest of sole relatively smooth with distinct subarticular tubercles at joints of most phalanges; relative length of toes: I < II < III < V < IV; foot webbing formula I0–1–II0–1+III0+–2IV2–1–V. Forearm short, less than one-third SVL; distance from tip of Finger III to proximal edge of palmar tubercle less than one-third SVL; metacarpal tubercles distinct, palmar tubercle round, about two times larger and more prominent than ovoid thenar tubercle; rest of palm with few supernumerary tubercles and distinct subarticular tubercles present at joints of most phalanges of Fingers II–IV; rela-

TABLE 1. MEASUREMENTS (IN MILLIMETERS) AND PROPORTIONS OF 20 FEMALES AND 20 MALES OF *Atelopus vogli* FROM THE TYPE LOCALITY, AND 34 FEMALES AND 60 MALES OF *Atelopus cruciger* FROM NINE LOCALITIES AS SHOWN IN FIGURE 1. The mean is followed by one standard deviation and the range in parentheses. For specimens measured, see Appendix 1.

	<i>Atelopus vogli</i>		<i>Atelopus cruciger</i>	
	Females	Males	Females	Males
SVL	37.0 ± 1.4 (33.4–39.0)	26.1 ± 2.4 (21.0–29.3)	44.3 ± 4.3 (39.5–49.9)	30.2 ± 1.7 (28.2–34.6)
HDWD	9.0 ± 0.3 (8.5–9.8)	7.1 ± 0.4 (6.3–7.7)	10.4 ± 0.7 (9.6–11.3)	8.1 ± 0.4 (7.4–8.8)
HLSQ	10.5 ± 0.6 (9.9–11.1)	8.1 ± 0.6 (6.4–8.8)	11.7 ± 0.9 (10.5–13.2)	9.5 ± 0.5 (8.3–10.5)
EYDM	3.4 ± 0.2 (2.9–3.8)	3.0 ± 0.2 (2.4–3.5)	4.0 ± 0.3 (3.8–4.5)	3.4 ± 0.2 (3.1–3.8)
ITNA	2.9 ± 0.2 (2.6–3.3)	2.4 ± 0.2 (1.9–2.8)	3.6 ± 0.3 (3.1–4.0)	2.8 ± 0.4 (2.3–3.4)
EYNO	2.9 ± 0.2 (2.7–3.2)	2.3 ± 0.2 (1.7–2.6)	3.2 ± 0.3 (2.9–3.8)	2.5 ± 0.3 (2.0–2.9)
SW	10.7 ± 0.5 (10.4–11.3)	7.0 ± 1.2 (6.0–8.5)	12.0 ± 2.0 (10.4–14.5)	8.0 ± 0.9 (7.0–9.3)
TIBL	17.4 ± 0.6 (16.1–18.3)	12.6 ± 0.8 (11.0–13.9)	20.0 ± 1.4 (18.4–22.2)	13.8 ± 2.5 (13.7–15.6)
FOOT	15.3 ± 0.7 (13.5–16.0)	10.3 ± 0.8 (8.7–11.6)	17.8 ± 2.3 (15.6–19.9)	12.2 ± 1.4 (10.7–14.0)
HAND	9.9 ± 0.6 (8.6–10.6)	6.6 ± 0.7 (5.3–7.7)	12.0 ± 1.3 (10.6–14.0)	8.2 ± 0.7 (7.3–9.3)
THBL	4.5 ± 0.2 (4.0–4.9)	3.1 ± 0.3 (2.4–3.4)	5.4 ± 0.7 (4.5–6.1)	3.9 ± 0.5 (3.2–4.2)
HDWD/SVL	0.24 ± 0.0 (0.23–0.26)	0.27 ± 0.0 (0.25–0.30)	0.23 ± 0.0 (0.22–0.25)	0.27 ± 0.0 (0.25–0.28)
HDWD/HLSQ	0.86 ± 0.0 (0.79–0.95)	0.88 ± 0.0 (0.82–0.98)	0.89 ± 0.1 (0.80–0.96)	0.85 ± 0.0 (0.81–0.91)
HLSQ/SVL	0.28 ± 0.0 (0.26–0.31)	0.31 ± 0.0 (0.29–0.34)	0.26 ± 0.0 (0.24–0.30)	0.31 ± 0.0 (0.29–0.33)
SW/SVL	0.29 ± 0.0 (0.26–0.30)	0.27 ± 0.0 (0.26–0.30)	0.28 ± 0.1 (0.25–0.29)	0.27 ± 0.1 (0.24–0.28)
TIBL/SVL	0.47 ± 0.0 (0.44–0.51)	0.48 ± 0.0 (0.43–0.54)	0.45 ± 0.0 (0.42–0.47)	0.45 ± 0.1 (0.45–0.51)
FOOT/TIBL	0.88 ± 0.0 (0.83–0.95)	0.82 ± 0.0 (0.75–0.86)	0.87 ± 0.46 (0.83–0.95)	0.86 ± 0.55 (0.83–0.90)
THBL/HAND	0.45 ± 0.0 (0.40–0.50)	0.46 ± 0.0 (0.42–0.53)	0.45 ± 0.0 (0.43–0.50)	0.47 ± 0.0 (0.43–0.54)
HAND/SVL	0.27 ± 0.0 (0.24–0.30)	0.25 ± 0.0 (0.21–0.28)	0.27 ± 0.0 (0.25–0.28)	0.27 ± 0.0 (0.25–0.28)

tive length of fingers: I < II < IV < III; thumb relatively short, distance from tip to outer edge of palmar tubercle less than half hand length; tips of Fingers II–IV slightly broadened; hand webbing formula  $10^+ - 1^+ III - 2^+ III_2 - 2IV$  (basal webbing between Fingers II and III, III and IV). Small rounded warts (partly conical) present on dorsolateral and lateral surfaces behind eye, continuing in a dorsolateral row along body, on posterior dorsum, and on dorsal surfaces of entire arm and leg, and tarsus; warts most dense

and most prominent around arm insertion and in a dorsolateral row.

In preservative, ground color greenish-tan, lighter on ventral side. All dorsal surfaces with dense brown vermiculation and well-defined cross-pattern posterior to head and an ill-defined chevron mark in sacral region; laterally with brownish band from nostril to eye and posterior to eye to groin (dark pattern absent ventrally including sole and palm). Toes I–II and Finger I almost completely tan as are tips of re-

TABLE 2. RESULTS OF TWO-FACTORIAL ANOVAs WITH MEASUREMENTS AS RESPONSE VARIABLES, PERFORMED FOR 20 FEMALES AND 20 MALES OF *Atelopus vogli* FROM THE TYPE LOCALITY, AND 34 FEMALES, AND 60 MALES OF *Atelopus cruciger* FROM NINE LOCALITIES AS SHOWN IN FIGURE 1. Highly significant results are in **bold faces**.

	Taxon		Sex		Taxon and sex combined	
	$F_{1,130}$	<i>P</i>	$F_{1,130}$	<i>P</i>	$F_{1,130}$	<i>P</i>
SVL	<b>187.24</b>	<0.001	<b>492.66</b>	<0.001	<b>14.4</b>	<0.001
HDWD	<b>104.41</b>	<0.001	<b>344.24</b>	<0.001	<b>6.4</b>	<0.001
HLSQ	<b>54</b>	<0.001	<b>162.4</b>	<0.001	0.48	0.5
EYDM	<b>51.45</b>	<0.001	<b>38.48</b>	<0.001	2.39	0.12
ITNA	<b>41.87</b>	<0.001	<b>66.86</b>	<0.001	4.82	0.03
EYNO	<b>11.54</b>	<0.001	<b>79.81</b>	<0.001	0.42	0.52
SW	<b>87.71</b>	<0.001	<b>22.49</b>	<0.001	<b>60.83</b>	<0.001
TIBL	<b>21.95</b>	<0.001	<b>194.19</b>	<0.001	8.06	0.005
FOOT	<b>24.02</b>	<0.001	<b>84.44</b>	<0.001	9.89	0.002
HAND	<b>73.85</b>	<0.001	<b>262.06</b>	<0.001	2.94	0.89
THBL	<b>71.24</b>	<0.001	<b>189.98</b>	<0.001	0.78	0.38

maining toes and fingers. Warts, tubercles, and tips of toes and fingers greenish-tan. Tongue cream without dark pigmentation. Coloration in life is unknown.

*Measurements and proportions of neotype (in mm).*—SVL 39.6; HDWD 9.6; HLSQ 11.0; EYDM 3.9; ITNA 3.3; EYNO 2.9; SW 10.4; TIBL 18.4; FOOT 16.3; HAND 11.1; THBL 4.9; HDWD/SVL 0.24; HDWD/HLSQ 0.87; HLSQ/SVL 0.28; SW/SVL 0.26; TIBL/SVL 0.46; FOOT/TIBL 0.89; THBL/HAND 0.44; HAND/SVL 0.28.

*Variation.*—All 192 additional specimens from nine localities are similar to the neotype. Variation includes dorsal snout shape, warts, foot and hand morphology, coloration, and measurements and proportions (Table 1). The tip of the snout in dorsal view may be more or less pointed. Similarly, warts can be more numerous and dense or less than in the neotype; warts may also continue onto outer dorsal surface of hand.

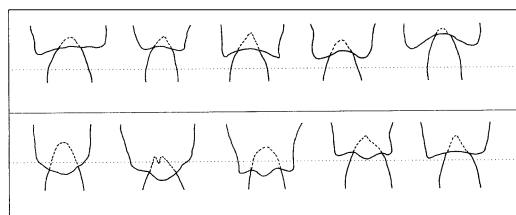


Fig. 4. Comparative schematic drawings of the ventral sphenethmoid/parasphenoid area in each of five specimens of *Atelopus vogli* (ZSM 285/1933/4, 1933/2, 1933/1, 1933/5, 1933/6) and *Atelopus cruciger* (ZSM 245/1929/1, 244/1929/1, 1929/3, 1929/2, 245/1929/2). The stippled line marks midway point between neopalatines and pterygoids (see text). Not to scale.

Toe III can be slightly shorter or longer than Toe V. Toe III may also have the webbing formula IIII. Some individuals have fewer or more subarticular tubercles (on both foot and hand) than the neotype. Others lack supernumerary tubercles on the palmar surface (instead, the surface is rugose). Webbing may be absent between Fingers III and IV.

In preservative, ground coloration varies from yellowish- to greenish-tan. In addition to the color pattern of the neotype, dorsal pattern variation also includes marbling, or rarely large dark areas; the cross-pattern behind the head may be less and the chevron mark in the sacral region may be more well defined (see figures in Mebs, 1980). The ventral side sometimes bears irregular dark flecks. According to descriptions of live individuals, ground color in *A. cruciger* is yellowish-green to olive, ventrally turning into yellowish cream or tan (without reddish markings), with tips of toes and fingers tan (or Toes I–II and Finger I occasionally completely tan); dorsal markings are brown or black (e.g., Rivero, 1961; Mebs, 1980; Lötters, 1996; senior author's personal observation on captive specimens).

Sexual dimorphism is indicated by females being larger (Tables 1–2), and males having a proportionally broader (HDWD/SVL) and longer (HLSQ/SVL) head (Table 1). The forearm in males is considerably thicker proximally than distally, and in most, Finger I has a nuptial excrescence.

*Distribution and life history.*—*Atelopus cruciger* has been reported from many different localities on both the northern and the southern versants of the central Cordillera de la Costa of Venezuela (Estados Aragua, Carabobo, Miranda, Vargas,

Yaracuy, and the Distrito Federal; Lötters, 1996; Manzanilla and La Marca, in press). Many of these localities lie within the Parque Nacional Henri Pittier (Manzanilla Puppo et al., 1995). In general, it may be stated that localities of *A. cruciger* are roughly situated at 10°20' to 10°40'N and 66°30' to 68°20'W (Fig. 1). Recently, Rivas Fuenmayor (1998) reported this toad also from Cerro Azul, a southernmost locality in Estado Cojedes (approximately 9°58'N, 68°37'W). This leads to the possibility that *A. cruciger* may be found throughout the entire mountainous area of the central coastal range (see Fig. 1). Rivero (1961) suggested that the area in which *A. cruciger* occurs eastward to Estado Sucre. However, this was questioned by La Marca (1992) and Lötters (1996). *Atelopus cruciger* inhabits lowland and humid montane forests at 100–2200 m above sea level (Lötters, 1996; Rivas Fuenmayor, 1998; Manzanilla and La Marca, in press). Sexton (1958) and Mebs (1980) studied behavioral aspects of this toad, indicating that it is diurnal, primarily terrestrial, and seasonally abundant along streams. Breeding along cascading streams was observed in April (M. Kneller, pers. comm.). Males appear to spend considerably more time along streams than females, and appear periodically throughout the year. Amplexus may last up to 19 days or even longer in captivity. Two females examined by us (under ZSM 244/1929 and ZSM 96/1930) contained about 150 eggs, tan in color, each about 1.0 mm in diameter, in each of their ovaries. The tadpole was described by Mebs (1980) as Type IV (cf. Orton 1953). Similar to other species of *Atelopus*, it belongs to the gastromyzophorous ecomorphological guild defined by Altig and Johnston (1989). Cocroft et al. (1990) described three different vocalization types similar to those of other species of the genus.

*Remarks.*—For about one decade now, it has repeatedly been stated that *A. cruciger* seems to have undergone drastic population declines (e.g., La Marca and Reinthaler, 1991; Manzanilla Puppo et al., 1995; La Marca and Lötters, 1997), although former reports indicate that this toad once was abundant (e.g., Sexton, 1958; Mondolfi, 1976; Mebs, 1980). A perusal of museum holdings revealed that no records of the species are held after 1988. Although, we and others have undertaken intensive searches for *A. cruciger* (both in- and outside the Parque Nacional Henri Pittier), it has not been seen in places where it previously occurred. Only a single population on the Caribbean versant of the coastal range has been detected (Anonymous, 2003).

Reasons for assumed population declines remain unknown; most localities seem not to have suffered from human impact. The current status of the populations of *A. cruciger* needs to be comprehensively investigated to develop conservation measures. The phenomenon of disappearance of Venezuelan *Atelopus* populations is not limited to the coastal mountain range. *Atelopus carbonerensis* (once very abundant in parts of the Cordillera de Mérida) has been observed on only three occasions since 1990, despite intensive collection efforts from scientists and locals (La Marca and Lötters, 1997; Torres and Barrio, 2001).

*Atelopus cruciger* is listed as endangered in the “Libro Rojo” of the Venezuelan fauna (Rodríguez and Rojas-Suárez, 1995); Manzanilla and La Marca (in press) recommended removing *A. cruciger* from its actual status and be placed in the category “critically endangered.” This category corresponds to those taxa that are facing an extremely high risk of extinction in the wild in the immediate future. The basis for this proposal, following the definitions and recommendations of the IUCN Red List Categories (IUCN, 2001, IUCN Red List Categories and Criteria: vers. 3.1. IUCN Species Survival Commission; <http://www.iucn.org/themes/ssc/redlists/redlistcatsenglish.pdf>), are an estimated reduction based on direct observation, of at least 80% over the last 10 years, a decline in the area of occupancy, extend of occurrence and the number of locations, plus deterioration of the quality of habitat of many populations, and a suspected effect of pathogens. The recommended IUCN red list citation for *A. cruciger* is CR A2ace; B1b(ii) (iv).

*Atelopus vogli* Müller  
Figures 2–3

*Atelopus cruciger vogli* Müller, 1934:151. Holotype: ZSM 3/1933 (Figs. 2–3), an adult female from “Schlucht Las Peñas (600 m), unweit von Maracay,” approximately at 10°17'00"N, 67°37'04"W; Müller, 1935:7; Rivero, 1961:173, 1964:311; Solano, 1969:21; Harding, 1983:56; Kluge, 1983:23; Lötters, 1996:23; Barrio Amorós, 1998:5.

*Atelopus varius vogli*: Peters, 1952:11.  
*Atelopus vogli*: Ginés, 1959:136.

*Diagnosis.*—An *Atelopus* with (1) SVL of adult females 33.4–39.0 mm ( $n = 20$ ), of adult males 21.0–29.3 mm ( $n = 20$ ); (2) snout pointed in dorsal view; upper jaw, in lateral view, protruding beyond lower; (3) neural spines externally visible; (4) long hind limbs (TIBL/SVL 0.43–

0.54,  $n = 40$ ), length of foot more than three-fourths length of tibia (FOOT/TIBL 0.83–0.95 in 20 females, 0.75–0.86 in 20 males); (5) tympanic membrane, tympanic ring, and ostia pharyngea absent; (6) small rounded warts (in part conical; no spiculae) present on dorsolateral and lateral surfaces posterior to eye, continuing in a dorsolateral row, on posterior dorsum, and on dorsal surfaces of entire arm and entire leg and partly on hand and tarsus; (7) outer and inner metatarsal and metacarpal tubercles present, remaining plantar and palmar surfaces free of tubercles, or palm with few supernumerary tubercles; distinct subarticular tubercles at joints of most phalanges of all toes and Fingers II–IV; (8) foot webbing formula  $I0-1-II0-1+III1-2IV2-0^+$  to  $1^+V$ ; hand webbing formula  $I0^+-1III1-2+III2-2IV$  (basal webbing between Fingers II–III, less or absent between III and IV); (9) thumb about half hand length (THBL/HAND 0.40–0.53,  $n = 40$ ), containing two phalanges; Finger III relatively long (HAND/SVL 0.21–0.30,  $n = 40$ ); tips of Fingers II–IV broadened; (10) in preservative, uniformly light to dark tan, usually with a brownish lateral band, and occasionally brownish marbling on head and hind limbs.

*Atelopus vogli* is most similar to *A. cruciger* from which it can be distinguished by its usually uniform tan dorsal coloration (adult *A. cruciger* always have dorsal markings; Fig. 2), smaller size (Tables 1–2), size of palmar and thenar tubercles (larger in *A. cruciger*; Fig. 3), and in characters of the sphenethmoid (Fig. 4). There are several other uniformly colored, “warty” *Atelopus* taxa from the northern Andes of South America (cf. Löters, 1996). *Atelopus vogli* can be distinguished from all of these by the presence of warts on entire arm and leg, basal hand webbing, and partly by the absence of spiculae and/or presence of two thumb phalanges.

*Description of holotype.*—Body slender; neural spines visible externally; head longer than broad; head length slightly less than one-third SVL; snout pointed in dorsal, with tip rounded, slightly depressed; in lateral aspect, upper jaw protruding beyond lower; nostril lateral, weakly protuberant and almost not visible from above; tongue more than three times longer than wide, broadest posteriorly, free for two-fifths of its length posteriorly; choanae small, rounded; ostia pharyngea absent; canthus rostralis straight from nostril to tip of snout, barely concave and longer from nostril to anterior corner of eye; eye width longer than distance from nostril to anterior corner of eye; loreal area barely concave; upper lip not fleshy; temporal area

straight; tympanic membrane and tympanic ring absent; dorsolateral postorbital (supratympanic) crest well developed, as long as eye width. Tibia long, slightly less than half SVL; foot shorter than tibia; metatarsal tubercles distinct, outer rounded, inner ovoid, about twice as large as the outer; rest of sole relatively smooth with distinct subarticular tubercles at joints of most phalanges; relative length of toes:  $I < II < III = V < IV$ ; foot webbing formula  $I0-1-II0-1+III1-2IV2-1-V$ . Forearm short, less than one-third SVL; distance from tip of Finger III to proximal edge of palmar tubercle almost one-third SVL; metacarpal tubercles distinct, palmar tubercle round, equal in size but more prominent than ovoid thenar tubercle; rest of palm weakly rugose with distinct subarticular tubercles present at joints of most phalanges of Fingers II–IV; relative length of fingers:  $I < II < IV < III$ ; thumb relatively short, distance from tip to outer edge of palmar tubercle less than half hand length; tips of Fingers II–IV slightly broadened; hand webbing formula  $I0-1III1-2+III2-2IV$  (basal webbing between Fingers II and III, III and IV). Small rounded warts present on dorsolateral and lateral surfaces posterior to eye, continuing in a dorsolateral row along body, and on dorsal surfaces of entire arm and leg, and hand and tarsus; warts most dense and most prominent around arm insertion and in a dorsolateral row (posterior of which are conical).

In preservative, uniform tan, darker around nostrils and upper loreal area, lighter on ventral side. Tip of snout yellowish-tan. Upper eyelid greenish tan. Warts and tubercles light tan. When freshly preserved, a brownish lateral band was visible from the nostrils to the eye and from behind the eye to the sacral region (Müller, 1934:152). Tongue cream without dark pigmentation. Coloration in life is unknown.

*Measurements and proportions of holotype (in mm).*—SVL 36.9; HDWD 9.0; HLSQ 11.0; EYDM 3.3; ITNA 3.0; EYNO 2.7; SW 10.5; TIBL 17.4; FOOT 14.5; HAND 10.0; THBL 4.5; HDWD/SVL 0.24; HDWD/HLSQ 0.82; HLSQ/SVL 0.30; SW/SVL 0.28; TIBL/SVL 0.47; FOOT/TIBL 0.83; THBL/HAND 0.45; HAND/SVL 0.27.

*Variation.*—All 415 additional topotypic specimens are similar to the holotype. Variation includes dorsal snout shape, warts, foot and hand morphology, coloration, and measurements and proportions (Table 1). The tip of the snout may be more acuminate. Warts vary in degree of prominence. Along flanks, warts may be nearly absent; on dorsal surface of hand, warts can be



lacking. In some specimens, warts are conical. Toe III can be slightly shorter or longer than Toe V. Foot webbing formula varies from  $-0+V$  to  $-1+V$ . Some individuals have fewer or more subarticular tubercles (on both foot and hand) than the holotype, and the palmar tubercle can be slightly larger than the thenar tubercle. Others have supernumerary tubercles on the palmar surface. Webbing may be absent between Fingers III and IV.

In preservative, coloration varies from uniform light to dark tan. Some individuals show a brownish marbled head pattern (with tip of snout yellowish-tan and upper eyelid greenish-tan) or traces of brownish marbling on the limbs. Marbling occasionally occurs on the outer sole and palm (with light tan tubercles and tips of fingers and toes). In most specimens, the brownish lateral band is visible.

Sexual dimorphism is indicated by females being larger (see Tables 1–2). Males have a proportionally broader (HDWD/SVL) and longer (HLSQ/SVL) head, and a shorter foot (FOOT/TIBL) than females (Table 1). The forearm in males is considerably thicker proximally than distally and, in most, Finger I has a nuptial excrescence.

*Distribution and life history.*—*Atelopus vogli* is known only from the type locality (Müller, 1934, 1935; Rivero, 1961) on the southern versant of the Cordillera de la Costa, Venezuela (Fig. 1). Müller (1935:8) reconsidered the type locality to be the cascades above the Río Güey, region of Las Peñas, near Hacienda La Trinidad, Estado Aragua, Maracay (approximately 700 m above sea level). Today, according to Manzanilla Puppo et al. (1995:297), this area is known as the “Poza del Diablo en las cabeceras del Río Güey.” In recent times, the natural vegetation of this area (humid forest) has suffered from human intervention, to the point that the original habitat has been drastically modified by repeated clearing and burning, with a savanna-like environment remaining. In the past, the site could have supported a seasonal (semideciduous) forest, like the ones present in a few nearby unaltered places.

*Atelopus vogli* is the only member of the genus known from this area. Together with the holotype, more than 400 specimens were collected. Eggs are visible through the skin of the venters of several females. Two females under ZSM 285/1933 (SVL 36.0 and 36.5 mm) had about 130 tan eggs, each about 1.0 mm in diameter, in each of their ovaries. This suggests that, during the date of collection, specimens congregated for breeding (which is seasonal in *Atelo-*

*pus*; Lötters, 1996). According to Müller (1934) and the ZSM catalog, in 1933 this was prior to June.

*Remarks.*—It is evident from the ZSM catalog that all specimens reported here were collected in 1933 by C. Vogl at the type locality and that all were shipped with the same lot (date of arrival 24 June 1933). After World War II, ZSM exchanged several specimens of *A. vogli* with other collections. We are aware of MCZ 20923–25, ULABG 3214 (formerly USNM 107328), UMMZ 92431 (formerly USNM 113267), USNM 107329–33 (Peters, 1952; Rivero, 1961, 1963b; Kluge 1983; Manzanilla Puppo et al., 1995), of which only ULABG 3214 was examined by us. This material increases the number of specimens collected and shipped together with the holotype to at least 426 [but probably more since ZSM 285/1933 and 285/1933/1–23 together were said to comprise 316 specimens (Solano, 1969:21)—they currently contain altogether only 299]. In contrast, the original description mentions a total of only approximately 70 specimens (Müller, 1934:10). The latter (except the holotype) are neither identifiable from the original description nor from the ZSM catalog. Although 115 of the specimens at ZSM (i.e., ZSM 350–464/1999) were uncataloged until recently (but have the date of arrival recorded), we conclude that the entire shipment by C. Vogl had been available to L. Müller, who was curator at ZSM when he described *A. vogli*. We consider all specimens collected together with the holotype as paratopotypes. Rivero (1961) reported the only known additional specimens of *A. vogli* (from the type locality), which may also represent exchanged paratypes (i.e., USNM 113265–66, 113268–74; not examined by us).

Because of apparent population declines in many *Atelopus* species throughout their distribution, the lack of recent records despite intensive searching (La Marca and Lötters, 1997 and references therein; J. Manzanilla and E. La Marca, unpubl. data) and the altered, only known locality for *A. vogli* (Manzanilla Puppo et al., 1995), this taxon is considered in an extremely high risk of extinction (if not already extinct). We propose it be placed in the category “critically endangered” of the IUCN Red List Categories (IUCN, 2001, IUCN Red List Categories and Criteria: version 3.1. IUCN Species Survival Commission; <http://www.iucn.org/themes/ssc/redlists/redlistcatsenglish.pdf>). Our rationale is based on an expected population reduction higher than 80% over at least more than one decade, where the reduction or its causes may not be reversible, based on a decline in the area

of occupancy and in the limited quality of habitat (see above). The geographic range within the area of occupancy is estimated to be less than 10 km<sup>2</sup>. The recommended IUCN red list citation for *A. vogli* is CR A2; B2a.

#### OSTEOLOGY

After several partial to synoptical contributions to the knowledge of the skeleton of *Atelopus* species (e.g., McDiarmid, 1971), Coloma (1997) reviewed the osteology of the genus. He provided a detailed general description of the *Atelopus* skeleton and noted variable characters among species, based on 51 taxa and published information. Regarding skull and pectoral girdle elements, our observations on *A. cruciger* from three separate localities largely agree with these data. Moreover, the available skeletons of *A. vogli* show identical states as *A. cruciger* in most characters. The two taxa differ, however, in ventral posterior sphenethmoid shape and extension (Fig. 4). Using the distance between neopalatines (anteriorly) and pterygoids (posteriorly) as a relative scale, the sphenethmoid reaches half this distance in five of seven *A. cruciger* examined (more than one-third in ZSM 244/1929/2 and ZSM 245/1929/2), but only in one of eight *A. vogli* (close to one half in ZSM 285/1933/7). Moreover, the posteroventral edge of the sphenethmoid is roughly concave in five of eight *A. vogli* (straight in ZSM 285/1933/3 and 285/1933/4; never convex) and convex in six of seven *A. cruciger* (slightly concave in one specimen only, ZSM 245/1929/2).

#### DISCUSSION

Lutz (1927) and Alemán (1952) used the name *Atelopus spumarius* Cope for *A. cruciger*. According to Lötters et al. (2002), the former is restricted to the upper Amazon basin and is morphologically different from *A. cruciger* (e.g., by adult size, skin texture, foot and hand morphology) and possess a middle ear (absent in *A. cruciger*). Some authors suggested *Atelopus bibronii* (O. Schmidt) to be a Venezuelan taxon related to *A. cruciger*, based on extremes of the color pattern of the latter (e.g., Günther, 1859 "1858"; Boulenger, 1882; Lutz, 1927). However, Savage (1972) designated a neotype for *A. bibronii*, clearly placing it as a junior synonym of the Central American *A. varius*, which differs from *A. cruciger* by having smooth skin and less webbed feet (Lötters et al., 1998).

Peters (1952) considered *A. vogli* to represent a subspecies of *A. varius* without providing reasons. Both are distinct taxa which differ consid-

erably in morphology and coloration (cf. Savage, 1972; Lötters et al., 1998). It is evident from the original description (Müller, 1934) and our results that *A. vogli* is most similar to *A. cruciger*. This led us and probably others to treat both species as identical (e.g., La Marca, 1992, 1997; Péfaur, 1992). However, our first ever comparison of material of both nominal forms involving specimens of *A. cruciger* from nine localities showed that there are consistent differences between *A. cruciger* and *A. vogli*. Besides skeletal features (see Osteology), the two differ in adult size, size of palmar and thenar tubercles, and dorsal pattern.

*Atelopus cruciger* is larger than *A. vogli*, with limited interspecific overlap in each sex (Table 1). ANOVA results in Table 2 show highly significant values with  $P < 0.001$  in all measurements each for "taxon" and "sex," and three such significant values when "taxon" and "sex" are combined (including SVL). Some other values are close to  $P = 0.001$ .

Palmar and thenar tubercles are about the same size in *A. vogli* (Fig. 3), or the palmar is slightly larger than the thenar tubercle. In *A. cruciger*, the palmar tubercle is about two times the size of the thenar tubercle (Fig. 3). The palmar tubercle in *A. vogli* is about half the size of that of *A. cruciger*, whereas its thenar tubercle is slightly smaller than that of *A. cruciger*.

None of the 416 specimens examined of *A. vogli* showed dorsal pattern (except in some individuals on the head), whereas 193 *A. cruciger* studied and those described or figured in publications from known localities did (e.g., Müller, 1934; Rivero, 1961; Mebs, 1980). In preservative, adult *A. cruciger* are characterized by a yellowish- to greenish-tan (ventrally lighter) color with a brown or black lateral band, and brown or black stipples, vermiculation or marbling on all dorsal surfaces, as well as a more or less defined cross-pattern behind the head and sometimes a chevron mark in the sacral region. Variation in color pattern is individual and we cannot support differences between populations as mentioned by Rivero (1961). In our opinion, the two color morphs described by this author simply represent contrasting intraspecific extremes. According to Rivero (1961), the only specimens of *A. cruciger* that lack dorsal markings are those of  $SVL \leq 15$  mm. We have not examined small specimens; but following Rivero (1961), we will not rule out that juveniles of *A. cruciger* and *A. vogli* cannot be distinguished.

Müller (1934) mentioned that Finger I is more slender in *A. vogli*. According to Rivero (1961), the latter in general is more slender, has a longer head, a more projecting snout, a lon-

ger and more slender Finger I, and less webbed toes than *A. cruciger*. We found that width of Finger I, snout and body shape, and foot webbing are variable and overlap in the two species.

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#### LITERATURE CITED

- ALEMÁN, G.C. 1952. Apuntes sobre reptiles y anfibios de la región Baruta-El Hatillo. Mem. Soc. Cienc. Nat. La Salle 12:11–30.
- ALTIG, R., AND G. F. JOHNSTON. 1989. Guilds of anuran larvae: relationships among developmental modes, morphologies, and habitats. Herpetol. Monogr. 3: 81–109.
- ANONYMOUS. 2003. Back from extinction: the rediscovery of the Rancho Grande Harlequin Frog (*Atelopus cruciger*) in Venezuela. Brit. Dendrobatid Grp. News. 49:21–22.
- BARRIO AMORÓS, C. L. 1998. Sistemática y biogeografía de los anfibios (Amphibia) de Venezuela. Acta Biol. Venez. 18:1–93.
- BOETTGER, O. 1893. Reptilien und Batrachier aus Venezuela. Ber. Senckenberg. Naturf. Gesell., Frankfurt am Main:35–42.
- BOULENGER, G. A. 1882. Catalogue of the Batrachia Salientia s. Ecaudata in the Collection of the British Museum. British Museum, London.
- COCROFT, R. B., R. W. MCDIARMID, A. P. JASLOW, AND P. M. RUÍZ-CARRANZA. 1990. Vocalizations of eight species of *Atelopus* (Anura: Bufonidae) with comments on communication in the genus. Copeia 1990:631–643.
- COLOMA, L. A. 1997. Morphology, systematics, and phylogenetic relationships among frogs of the genus *Atelopus* (Anura: Bufonidae). Unpubl. Ph.D. diss., Univ. of Kansas, Lawrence.
- , S. LÖTTERS, AND A. W. SALAS. 2000. Systematics of the *Atelopus ignescens* complex (Anura: Bufonidae): designation of a neotype of *Atelopus ignescens* and recognition of *Atelopus exiguus*. Herpetologica 56:303–324.
- DINGERKUS, G., AND L. D. UHLER. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. Stain Technol. 52: 229–232.
- DUELLMAN, W. E. 1999. Global distribution of amphibians: patterns, conservation, and future challenges, p. 1–30. In: Patterns of distributions of amphibians. A global perspective. W. E. Duellman (ed.). Johns Hopkins Univ. Press, Baltimore, MD.
- FROST, D. R. (ED.) 1985. Amphibian species of the world. A taxonomic and geographical reference. Allen Press, Inc., Lawrence, KS.
- GINÉS, H. 1959. Familias y géneros de anfibios—Amphibia—de Venezuela. Mem. Soc. Cienc. Nat. La Salle 19:84–146.
- GRAY, P., AND D. C. CANNATELLA. 1985. A new species of *Atelopus* (Anura, Bufonidae) from the Andes of northern Perú. Copeia 1985:910–917.
- GÜNTHER, A. 1859 (“1858”). Catalogue of the Batrachia Salientia in the Collection of the British Museum. British Museum, London.
- HARDING, K. A. 1983. Catalogue of New World amphibians. Pergamon Press, Oxford.
- ICZN. 2002. Opinion 2013 (Case 3137). *Phrynidium crucigerum* Lichtenstein and Martens, 1856 (currently *Atelopus cruciger*; Amphibia, Anura): proposed conservation of the specific name by the designation of a neotype. Bull. Zool. Nomencl. 59:226–227.
- KLUGE, A. G. 1983. Type-specimens of amphibians in the University of Michigan Museum of Zoology. Misc. Publ. Mus. Zool., Univ. Mich. 166:1–68.
- LA MARCA, E. 1992. Catálogo taxonómico, biogeográfico y bibliográfico de las ranas de Venezuela. Cuad. Geogr., Univ. Los Andes, Mérida 9:1–197.
- . 1997. Lista actualizada de los anfibios de Venezuela, p. 103–120. In: Vertebrados Actuales y Fósiles de Venezuela, Ser. Catálogo Zool. Venezuela 1. E. La Marca (ed.). Museo de Ciencia y Tecnología, Mérida, Venezuela.
- , AND S. LÖTTERS. 1997. Monitoring of declines in Venezuelan *Atelopus* (Amphibia: Anura: Bufonidae), p. 207–213. In: Herpetologia Bonensis. W. Böhme, W. Bischoff, and T. Ziegler (eds.). Societas Europaeae Herpetologicae, Bonn, Germany.
- , AND H. P. REINTHALER. 1991. Population changes in *Atelopus* species of the Cordillera de Mérida. Herpetol. Rev. 22:125–128.
- , J. E. GARCÍA-PÉREZ, AND J. M. RENJIFO. 1990 (“1989”). Una nueva especie de *Atelopus* (Amphibia: Anura: Bufonidae) del Páramo de Tamá, Estado Apure, Venezuela. Caldasia 16:97–104.
- LEVITON, A. E., R. H. GIBBS JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in Herpetology and Ichthyology. Part I. Standard symbolic codes for institutional resource collections in Herpetology and Ichthyology. Copeia 1985:802–832.
- LICHTENSTEIN, M. H. C., AND E. MARTENS. 1856. Nomenclator Reptilium et Amphibiorum Musei Zoologici Berolinensis. Akademie der Wissenschaften, Berlin, Germany.
- LÖTTERS, S. 1996. The Neotropical toad genus *Atelopus*. Checklist—biology—distribution. Vences and Glaw, Cologne, Germany.
- , AND E. LA MARCA. 2001: case 3173. *Phrynidium crucigerum* Lichtenstein and Martens, 1856 (currently *Atelopus cruciger*; Amphibia, Anura): proposed conservation of the specific name by the designation of a neotype. Bull. Zool. Nomencl. 58:119–121.
- , W. BÖHME, AND R. GÜNTHER. 1998. Notes on the type material of the Neotropical Harlequin Frogs *Atelopus varius* (Lichtenstein and Martens, 1856) and *Atelopus cruciger* (Lichtenstein and Martens, 1856) deposited in the Museum für Naturkunde of Berlin (Anura, Bufonidae). Mitteil. Mus. Naturkd. Berlin (Zool. Reihe) 74:173–184.
- , W. HAAS, S. SCHICK, AND W. BÖHME. 2002. On the systematics of the Harlequin Frogs (Amphibia:

- Bufoinae: *Atelopus*) from Amazonia. II. Redescription of *Atelopus pulcher* (Boulenger, 1882) from the eastern Andean versant in Peru. *Salamandra* 38: 165–184.
- LUTZ, A. 1927. Notas sobre batrachios da Venezuela e da Ilha de Trinidad. *Mem. Inst. Oswaldo Cruz* 20: 35–65.
- LYNCH, J. D. 1993. A new Harlequin Frog from the Cordillera Oriental of Colombia (Anura, Bufonidae, *Atelopus*). *Alytes* 11:77–86.
- MANZANILLA, J., AND E. LA MARCA. In Press. Museum records and field samplings as sources of data pointing to population crashes for *Atelopus cruciger*, a proposed critically endangered species from the Venezuelan coastal range. *Memoria, Fundación La Salle, Caracas, Venezuela*.
- MANZANILLA PUPPO, J., A. FERNÁNDEZ-BADILLO, E. LA MARCA, AND R. VISBAL GARCÍA. 1995. Fauna del Parque Nacional Henri Pittier, Venezuela: composición y distribución de los anfibios. *Acta Cient. Venez.* 46: 294–302.
- MCDIARMID, R. W. 1971. Comparative morphology and evolution of frogs of the Neotropical genera *Atelopus*, *Dendrophryniscus*, *Melanophryniscus*, and *Oreophrynella*. *Sci. Bull. Los Angeles Co. Mus. Nat. Hist.* 12:1–66.
- MEBS, D. 1980. Zur Fortpflanzung von *Atelopus cruciger* (Amphibia. Salientia. Bufonidae). *Salamandra* 16: 65–81.
- MONDOLFI, E. 1976. Fauna silvestre de los bosques húmedos tropicales de Venezuela, p. 113–181. In: *Conservación de los bosques húmedos de Venezuela*. Anonymous (ed.). Sierra Club-Consejo de Bienestar Rural, Caracas, Venezuela.
- MÜLLER, L. 1934. Über eine neue Rasse von *Atelopus cruciger* (Licht. u. Marts) von Venezuela. *Zool. Anz.* 108:145–155.
- . 1935. Sobre una nueva raza de “*Atelopus cruciger*” Licht. & Marts. de Venezuela. *Acad. Cienc. Fís., Mat. Nat.* 1–10.
- 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. *Am. Mus. Nat. Hist. Novit.* 2752:1–32.
- NIEDEN, F. 1926. Anura II. Das Tierreich. Walter de Gruyter and Co., Berlin, Germany.
- ORTON, G. L. 1953. The systematics of vertebrate larvae. *Syst. Zool.* 2:63–75.
- PÉFAUR, J. E. 1992. Checklist and bibliography (1960–85) of the Venezuelan herpetofauna. *Smiths. Herpetol. Info. Serv.* 89:1–54.
- PETERS, J. A. 1952. Catalogue of the type specimens in the herpetological collections of the University of Michigan Museum of Zoology. *Occas. Pap. Mus. Zool., Univ. Mich.* 539:1–55.
- PLÖSCH, T. 1991. Die Alizarin-/Alcianblau-Färbung nach Dingerkus and Uhler. *DATZ* 44:252–254.
- POUNDS, J. A., AND M. L. CRUMP. 1994. Amphibian declines and climate disturbance: the case of the Golden Toad and the Harlequin Frog. *Conserv. Biol.* 8:72–85.
- RIVAS FUENMAYOR, G. 1998. Geographic distribution. Anura. *Atelopus cruciger*. *Herpetol. Rev.* 29:172.
- RIVERO, J. A. 1961. Salientia of Venezuela. *Bull. Mus. Comp. Zool. Harvard* 126:1–207.
- . 1963a. Five new species of *Atelopus* from Colombia, with notes on other species from Colombia and Ecuador. *Carib. J. Sci.* 3:103–124.
- . 1963b. The distribution of Venezuelan frogs. II. The Venezuelan Andes. *Ibid.* 3:87–102.
- . 1964. The distribution of Venezuelan frogs. IV. The coastal range. *Ibid.* 4:307–319.
- RODRÍGUEZ, J. P., AND F. ROJAS-SUÁREZ. 1995. Libro Rojo de la Fauna Venezolana. Provita, Caracas, Venezuela.
- RON, S. R., W. E. DUELLMAN, L. A. COLOMA, AND M. R. BUSTAMANTE. 2003. Population decline of the Jambato Toad *Atelopus ignescens* (Anura: Bufonidae) in the Andes of Ecuador. *J. Herpetol.* 37:116–126.
- SAVAGE, J. M. 1972. The Harlequin Frogs, genus *Atelopus*, of Costa Rica and western Panama. *Herpetologica* 28:77–94.
- , AND R. W. HEYER. 1969. Variation and distribution of the tree frog genus *Phyllomedusa* in Costa Rica, Central America. *Beitr. Neotrop. Fauna* 5: 111–131.
- , AND ———. 1997. Digital webbing formulae for anurans: a refinement. *Herpetol. Rev.* 28:131.
- SEXTON, O. 1958. Observations on the life history of a Venezuelan frog, *Atelopus cruciger*. *Acta Biol. Venez.* 2:235–242.
- SOLANO, H. 1969. Beiträge zur Kenntnis der Amphibienfauna Venezuelas. *Veröffentl. Zool. Staatssamml. München* 13:1–26.
- TORRES, D. A., AND C. L. BARRIO. 2001. Geographic distribution. Anura. *Atelopus carbonerensis* (La Carbonera Harlequin Toad; Sapito Arlequín de la Carbonera). *Survivorship. Herpetol. Rev.* 32:179.
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## APPENDIX 1

## MATERIAL EXAMINED

Cleared and stained material is indicated by (C & S). Specimens used for morphometric analysis are indicated by (M).

*Atelopus cruciger*.—ZSM 245/1929 (12 specimens), 245/1929/1–2 (C & S), 245/1929/3–5 (M), Caracas,

- Distrito Federal [locality 1 in Fig. 1]; FMC 170 (M), 265 (M), 540 (M), 1072 (M), 4077 (M), 4345 (M), 4369 (M), 4711–12 (M), 5350 (M), Planta Eléctrica de Naguayatá, Distrito Federal (720 m) [locality 2 in Fig. 1]; FMC 440 (M), 457 (M), 460–61 (M), 463–64 (M), 466 (M), 472 (M), 608 (M), 641 (M), 837 (M), 839 (M), 1164 (M), 1167 (M), 1169 (M), 1171–72 (M), 1305 (M), 1307–08 (M), 1311–12 (M), 1315–16 (M), 1318 (M), 1322 (M), 1326 (M), 1329 (M), 1331 (M), 1980 (M), 1982 (M), 1986 (M), 1994 (M), 2002–03 (M), 2013 (M), 2021 (M), 2025–27 (M), 2029 (M), 2171 (M), 2179–81 (M), 2186 (M), 2193 (M), 2281 (M), 2493 (M), 2646 (M), 2654 (M), 2680 (M), 2725 (M), 3768 (M), 4697 (M), 4962–63 (M), 4980–82 (M), 4989, 4991 (M), Curupao, Estado Miranda (1115 m) [locality 3 in Fig. 1]; SMF 45097/9 (3 specimens), Los Teques, Estado Miranda [locality 4 in Fig. 1]; ZSM 96/1930/1 (C & S), 96/1930/2–5 (M), La Cumbre, Estado Aragua [locality 5 in Fig. 1]; KU 166667–68 (M), 166675–76 (M), 185704 (M), 185706 (M), 185708 (M), km 26–29 on Maracay-Ocumare-road, Estado Aragua (650 m) [locality 6 in Fig. 1]; KU 132914–15 (M), 166679 (M), SMF 30635 (M), 57653 (M), ZFMK 37328–30 (M), ZSM 93/1947 (43 specimens), 93/1947/1–9 (M), 93/1947/10 (neotype) (M), Rancho Grande and vicinity, Estado Aragua (1000–1100 m) [locality 7 in Fig. 1]; ZSM 244/1929 (6 specimens), 244/1929/1–4 (C & S), 244/1929/5–10 (M), near Lago Valencia, Estado Aragua or Carabobo [locality 8 in Fig. 1]; SMF 4085 (2 specimens) (M), Puerto Cabello, Estado Carabobo [locality 9 in Fig. 1].
- Atelopus vogli*.—ZSM 3/1933 (holotype) (M), 285/1933 (276 specimens), 285/1933/1–8 (C & S), 285/1933/9–23 (M), 350–373/1999 (M), 374–464/1999, ULABG 3214, Las Peñas region, Estado Aragua (600–700 m).