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Distribution of *Strabomantis biporcatus* (Terrarana: Strabomantidae) in northern Venezuela, with comments on its phenotypic variation

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Abstract. Phenotypic variation in an eastern population of the broad-headed frog *Strabomantis biporcatus* is presented, along with comments on morphological variation among the species, compared with the best known central Venezuelan populations. The distribution of the species, based on voucher specimens and personal observations, is mapped.

Key words. Amphibia, Anura, *Strabomantis biporcatus*, distribution, variation, morphology, Venezuela.

Even as recent revisions of the taxonomy of Central and South American strabomantid frogs (SAVAGE & MYERS 2002, CRAWFORD & SMITH 2005, HEINICKE et al. 2007; HEDGES et al. 2008) have considerably improved our understanding of the evolutionary relationships in this diverse and unwieldy group, navigating through multiple name changes and tracking their impact on distribution data has been tricky. A case in point is the northern Venezuelan broad-headed strabomantid frog with the specific epithet *biporcatus*, whose generic placement originated with *Strabomantis* (PETERS 1863) and *Hylodes* (BOETTGER 1893) before settling into *Eleutherodactylus* (STEJNEGER 1904) for over a century until 2002 (SAVAGE & MYERS 2002). Remarkably, during only the last five years the species progressed from *Eleutherodactylus* via *Craugastor* to the original *Strabomantis*. Because of these taxonomic adjustments and because of our sighting of a highly atypical color variant, we here assemble the most recent distribution data for the species, comment on its phenotypic diversity, and outline its taxonomic history to clarify its position.

In their careful revision of Central and northern South American broad-headed

Eleutherodactylus in the *biporcatus* species group, SAVAGE & MYERS (2002) concluded that the use of the name *E. maussi* (BOETTGER) for northern Venezuelan broad-headed *Eleutherodactylus* is inappropriate. Instead, SAVAGE & MYERS (2002) suggested that *Strabomantis biporcatus* Peters, the name of a broad-headed species in Central America, took precedence. These authors convincingly demonstrated that Central American populations of *Eleutherodactylus biporcatus* comprised several different species, requiring the resurrection of *E. gulosus* (COPE), *E. megacephalus* (COPE), and *E. rugosus* (PETERS). They also noted that the type series used by WILHELM PETERS to describe *E. biporcatus* (erroneously cited as collected in Veragua, Panamá) actually represents the Venezuelan species *E. maussi*.

It is therefore clear that the correct name for Venezuelan populations of broad-headed *Eleutherodactylus* is the oldest available name, *E. biporcatus*, and not *E. maussi*. More recently, CRAWFORD & SMITH (2002) resurrected the genus *Craugastor*, including the *biporcatus* group, from subgenus level. Lastly, further refinements of molecular approaches (HEINICKE et al. 2007, HEDGES et al. 2008) al-

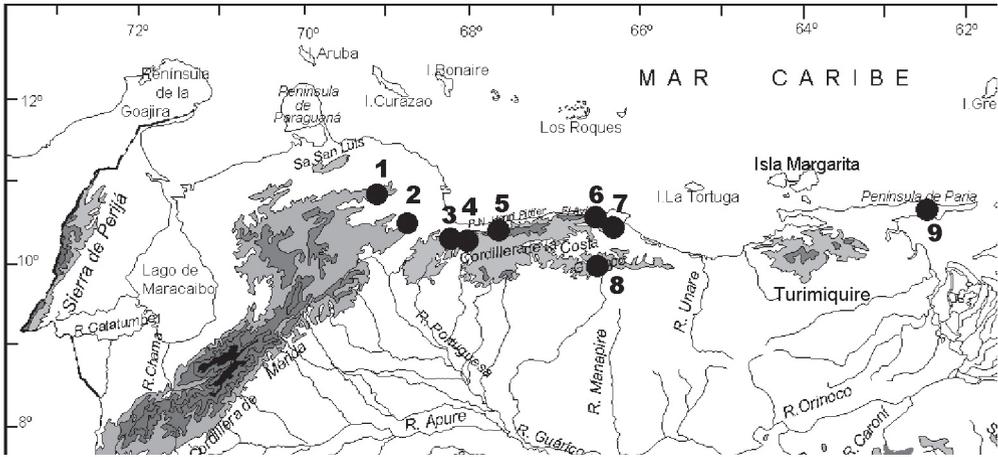


Fig. 1. Map of northern Venezuela showing localities for *Strabomantis biporcatus* from both the literature and voucher specimens. Shades correspond with the following altitudes: white: below 500 m; light grey: from 501 to 1500 m; dark grey: from 1501 to 3500 m; black: above 3500 m. Localities (see complete reference in the text): 1. Estado Falcón, Parque Nacional Cueva Quebrada del Toro; 2. includes Estado Yaracuy, Hacienda El Jaguar, 15 km NNW Aroa, and Río Guayabito, Parque Nacional Yurubí; 3. Estado Carabobo, San Esteban, Bárbula; 4. includes Estado Carabobo, Cerro Pelón; and Campamento Palmichal, Pico San Marcos; 5. Estado Aragua, Rancho Grande; 6. Estado Vargas, Canales de Naiguatá; 7. includes Estado Miranda, Capaya, and Hacienda Santa Rosa; 8. Estado Miranda, Guatopo; 9. Estado Sucre, Las Melenas, Paria.

lowed confident placement of the species into *Strabomantis*. Some of these name changes are reflected in recent check-lists (e.g., *Craugastor* was used by BARRIO-AMORÓS [2004] and FROST [2006]) as authors attempted to keep up with the rapid evolution of the nomenclature.

Because of this taxonomic adjustment and because of our sighting of a highly atypical color variant, we here review the species' distribution and its phenotypic variation across Venezuela to ensure the proper future application of the correct species name across the range of *S. biporcatus*. The species is also of interest because it is the only proper South American species in the genus, separated from the others by the Andes (CRAWFORD & SMITH 2005, HEINICKE et al. 2007). Throughout, the following institutional acronyms are used: Colección de Vertebrados, Universidad de los Andes, Mérida, Venezuela (CVULA); Fundación AndígenA Photographic and Phonographic Collection (FA); Museo de la

Estación Biológica Rancho Grande, Maracay, Venezuela (EBRG); Museo de Historia Natural La Salle, Caracas, Venezuela (MHNLS).

Distribution. There are few published distributional accounts for *S. biporcatus*, almost all reported under the older synonym *E. maussi* (LYNCH 1975, LA MARCA 1992), and with only two localities widely mentioned: Rancho Grande, Estado Aragua, and San Esteban, Estado Carabobo (LYNCH 1975). The type locality, Puerto Cabello, is actually most likely merely the port from which the shipment of specimens originated (LA MARCA 1992); it certainly does not contain potential habitat for *S. biporcatus* and we therefore do not include the locality in our considerations. BARRIO-AMORÓS (1998) mentioned several other localities based on his own field experience, or in personal collections (v. e. M GONZÁLEZ SPONGA), but no vouchers were mentioned. A further locality, Guatopo National Park, was mentioned by SAVAGE & MYERS (2002), who did not include in their

account the already mentioned sites by BARRIO-AMORÓS (1998).

Rancho Grande is a biological research station situated within the cloud forest of the Cordillera de la Costa (DUELLMAN 1979, BARRIO-AMORÓS 2006). This is a typical habitat for the species, and *S. biporcatus* has been collected and observed at this locality for decades (e.g., HEATWOLE 1962, SCHMID et al. 1992, BARRIO-AMORÓS 2006, and pers. obs., see Appendix). This area falls into the biogeographic region termed “región orocostense” by BARRIO-AMORÓS (1998). The Guatopo locality (Fig. 1) is in the Serranía del Interior and in the same main biogeographic region, although in a different and smaller coastal mountain chain, at a lower elevation (600 m). MANZANILLA et al. (1996) were the first to report the species from the Península de Paria (Estado Sucre) in the northeastern extreme of Venezuela, an eastward range extension of over 400 km. The Paria locality of MANZANILLA et al. (1996) lies in coastal cloud forest at an elevation of about 1150 m. RIVERO & MIJARES-URRUTIA (2004) recently reported the species from the Parque Nacional Cueva Quebrada del Toro in Estado Falcón, the northern and westernmost known locality.

Although specimen locality data indicated that the distribution of *S. biporcatus* in northern Venezuela is discontinuous, we assume that the species is likely much more broadly distributed than the literature and available museum specimens would indicate. This notion is based on the presence of suitable high-altitude habitats throughout the mountainous coastal region. As attested to by preserved specimens (see Appendix), *S. biporcatus* occurs in Venezuela in cloud forests of the northern coastal range (from 250 m to at least 1600 m in elevation) in the states of Aragua, Carabobo, Falcón, Miranda, Vargas and Yaracuy (and very probably also in Cojedes, Distrito Federal, and Guárico). The presence of this species in the Península de Paria in Estado Sucre, a region quite distant from the central coastal range, is especially interesting, as the Paria locality is separated by a dry val-

ley (the Unare river depression) and by an air distance of about 400 km from Pacaya, the closest known verified locality.

Considering the geography of the mountainous chain that parallels the Caribbean Sea across much of northern Venezuela, it appears that medium to high-altitude localities with cloud forest habitat appropriate for *S. biporcatus* exist in a patchy distribution all the way from the Península de Paria in the east to the western Coastal Range of Venezuela (Fig. 1). The verified presence of populations of *S. biporcatus* in the central coastal range and the Península de Paria lead us to hypothesize that this species should also be present in the Turimiquire, the highest mountain massif east of the central coastal range from which it is separated by the Unare depression (Fig. 1). The Turimiquire area has not yet been well explored, although it is known to have a high degree of endemism and no amphibian species here are shared with the central coastal range (BARRIO-AMORÓS, 1998). We believe that additional research in this area might produce further localities for *S. biporcatus*. The only frogs with broader ranges in montane regions throughout Venezuela are either taxa most likely comprising complexes of cryptic species (e.g., *Hyalinobatrachium orientale*, *Mannophryne* aff. *trinitatis* but not *M. trinitatis* sensu stricto [see BARRIO-AMORÓS et al. 2006a], *Eleutherodactylus bicumulus*) or introduced species (e.g., *E. johnstonei*; KAISER et al. 2002). The issue of localities is further complicated by the fact that in some cases accurate locality assignments are lacking. Preliminary data suggests that the Paria cloud forest amphibians are distinct from those of the Central Coastal range (as also found in *Allobates bromelicola* and *A. caribe*, another pair of similar species from these two ranges [BARRIO-AMORÓS et al. 2006b]), or they had not enough time to differ.

Color variation. During an expedition to the Península de Paria (northeastern extreme of Venezuela) in September 2001, we saw and photographed a large female of broad-headed *Strabomantis* (Fig. 2A), a

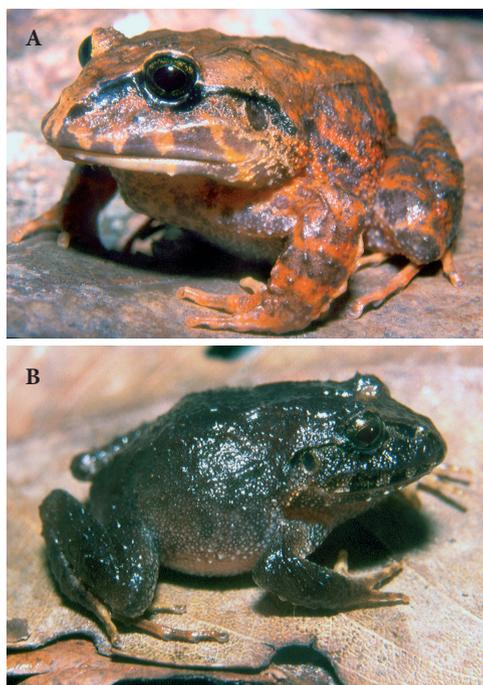


Fig. 2. Specimens of *Strabomantis biporcatus* from the Península de Paria in northeastern Venezuela. (A) Female, SVL 65 mm. (B) Male, SVL 32 mm. Photographs by CÉSAR L. BARRIO-AMORÓS.

young female, and a series of juveniles. The color of the female was so completely different from the central Cordillera de la Costa morphotype that it initially led us to speculate about the presence of an undescribed broad-headed species endemic to the Península de Paria. However, after comparing preserved museum specimens from Paria with others from more central localities, we conclude that all specimens belong to *S. biporcatus*. The color variant, however, is of interest.

In their account of *Eleutherodactylus biporcatus* coloration, SAVAGE & MYERS (2002) provide a description of central northern Venezuelan populations based on preserved material (J. M. SAVAGE, pers. comm.). In general, adult *S. biporcatus* from Rancho Grande and Guatopo are dark to pale brown above and light tan to whitish in ventral surfaces. In life, they are mostly dark brown to blackish

dorsally (Fig. 2B), although sub adults can be leaf mimics in brown and reddish (see photos in BARRIO-AMORÓS 2006: 10). The following description of the color of a female Paria individual is based on slides (FA Fundación Andígena-176-80; Fig. 2A). This is a large specimen (adult female of 65 mm SVL), reflecting the considerable sexual dimorphism of the species: adult males have vocal slits and are considerably smaller, ranging in size from 30–38 mm SVL (SAVAGE & MYERS 2002). This female was orange-brown above in life with interspersed orange reticulations including the dorsal plicae, outlined by brown lines. The head is of the same color as the dorsum all the way to the tip of the snout. A broad black canthal stripe separates the above color from the loreal region, which is orange crossed by four grey triangular bars that diffuse before reaching the eye. The canthal stripe continues below the eye and extends into a supratympanic black stripe. The tympanum is dark brown and is surrounded dorsally by a supratympanic fold and ventrally by an area tending to orange. The lower lips are dark cream-colored and lack bars. Forelimbs and hind limbs are bright orange and crossed by grey bars. The ulnar, irregular fold is whitish. The posterior dorsal back



Fig. 3. Females of *Strabomantis biporcatus* from Rancho Grande, Central Cordillera de la Costa of Venezuela, showing the rather more elevated dorsal plicae than in specimens from the Península de Paria. These provide Central Cordillera individuals with a much more rough-skinned appearance. Photograph by CÉSAR L. BARRIO-AMORÓS.

is a paler brown with orange intrusions. The flanks are orange with irregular grey reticulations. The venter is white, the throat whitish with grey spots.

Specimens EBRG 2386 and 2498 (see Appendix) are both females from Cerro el Humo, the highest peak (elevation up to 1150 m) on the Península de Paria. These individuals have SVLs of 56.5 mm and 48.6 mm, respectively. Although we did not see these individuals in life and field notes are apparently lacking, they appear largely congruent with our description of the living female above. These preserved animals are pale to dark brown dorsally with whitish flanks, forelimbs, and hind limbs, and we presume that these were orange in life and crossed by dark grey bars. The lateral surfaces of the head are dark brown, with whitish bars. EBRG 2498 has a lighter interorbital bar; the throat is whitish, spotted with pale brown. The chest and venter are whitish. The inferior surfaces of the posterior part of the thighs are mottled with small brown spots. EBRG 2386 is considerably different ventrally. The throat in this individual is pale brown with scattered whitish spots (usually corresponding to tubercles), the chest is whitish with a large area of pale brown marbling, and with a whitish venter with small brown spots. The inner tibia is crossed by the same kind of dark brown bars as crosses the upper surfaces, although narrower. This pattern is very different from the more darkish brown or grey typical of the central populations. Some young specimens from Paria were quite different, being very dark dorsally (Fig. 2B) and brown to dirty white ventrally. There is merely a hint of an orange coloration in the interorbital area and along the fingers and toes. These individuals conform much more closely to phenotype of *S. biporcatus* from the central coastal Cordillera, although they are much less tuberculate and the plicae are less protuberant (also seen in BARRIO-AMORÓS 2006: 10). Two juveniles seen had SVLs of 26 and 15 mm. One was dark dorsally, and the smaller one was light grey, with darker plicae, and bars on fore-

limbs and legs; ventrally it was whitish. We speculate that there may be some kind of ontogenetic color change in the species, especially in females. All of the specimens from central populations we studied corroborate the description of SAVAGE & MYERS (2002).

Variation in other characteristics. A few exterior features of *S. biporcatus* from the Península de Paria are dissimilar from those found in populations from the central coastal Cordillera, although these differences can clearly be based on intraspecific variation. For example, dorsal plicae in preserved Paria animals are low in contrast to the very distinct and elevated plicae of populations from the central coastal Cordillera; the latter can be felt on the specimens and seen in photographs (e.g., Fig. 3; BARRIO-AMORÓS 2006: 10). An inner tarsal fold is present, but less distinct as in populations from the central coastal Cordillera. The known size of Paria individuals is somewhat smaller (to 65 mm SVL) than animals from the central coastal Cordillera (up to 74 mm recorded by SAVAGE & MYERS, 2002), although the actual sample size is very small to state this character. EBRG 2386 is ventrally coarsely granular, whereas EBRG 2498 is slightly areolate.

Natural history. We saw the animals during the day in the forest litter. They were not active, but hidden (large female) and moved when disturbed. Juveniles were seen in a dry stream bed with high leaf litter humidity and occurred syntopically with individuals of *Allobates caribe* (BARRIO-AMORÓS et al. 2006b). A subadult female (being deposited at EBRG) of 44 mm, was accidentally stepped on and died on a recent expedition to Paria. It had in its stomach a large grasshopper of almost 20 mm length.

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Appendix

Specimens examined

Strabomantis biporcatus. VENEZUELA: Estado Aragua: Rancho Grande, elevation 1000 m, CVULA 2726-67; Rancho Grande, elevation 1200 m, EBRG 68-69, 1198. Estado Carabobo: Campamento Palmichal, Pico San Marcos, elevation 780 m, EBRG 2303; Bárbula, elevation 1000 m, MHNLS 3680; Cerro Pelón, La Florida, Serranía de Barbula, elevation 1100 m, MHNLS 4799. Estado Miranda: La Toma, Capaya, elevation 250 m, MHNLS 3116-67. Estado Sucre: Cerro el Humo, NE Las Melenas, Península de Paria, elevation 1100 m, EBRG 2386, 2498. Estado Vargas: Canales de Naguayá, elevation 720 m, MHNLS 11439. Estado Yaracuy: Hacienda El Jaguar, 15 km NNW Aroa, elevation 700 m, EBRG 2796.

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