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Discovery of the frog genus *Anomaloglossus* in Panama, with descriptions of two new species from the Chagres Highlands (Dendrobatoidea: Aromobatidae)

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ABSTRACT

The occurrence in Panama is documented for the South American frog genus *Anomaloglossus* (Dendrobatoidea: Aromobatidae). Two species are described from a low, forested uplift in east-central Panama, just northeast of Panama City. These low mountains, unnamed on maps, are designated the “Chagres Highlands” because a large part of the uplift lies in the Río Chagres drainage (which provides water critical to lock operation in the Panama Canal). The Chagres Highlands may be a lower montane forest refuge for some amphibians and reptiles, including the two *Anomaloglossus* and *Atelopus limosus*, and the rare snakes *Atractus depressiocellus*, *A. imperfectus*, *Geophis bellus*, and *Rhadinaea sargenti*. Several other rare species are not endemic but include the Chagres Highland area as part of their individually fragmented or mosaic distributions (*Adinobates fulguritus*, *Anolis kunayalae*, *Coniophanes joanae*, *Geophis bracycephalus*, *Dipsas nicholsi*).

The two new frogs are at least broadly sympatric in the Chagres Highlands, but both species are rare. *Anomaloglossus astralogaster*, new species, is known only from the adult female holotype (22 mm SVL). Its ventral surfaces are covered overall with whitish dots (≤ 0.1 mm) somewhat similar to large chromatophores but possibly glandular; there is no appearance of

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glandular structure at $\times 50$ magnification, but the edges of some of the pale dots can be “felt” with a fine (0.1 mm diameter) teasing needle and histological examination is needed.

The other taxon is *Anomaloglossus isthminus*, new species, which is described from six specimens including four adult males (19–21 mm SVL), one adult female (23 mm SVL), and a juvenile female. Dorsal surfaces are basically brown mottled with darker brown. Small pale yellowish spots located proximally above the insertions of arm and thigh are not well defined and tend to disappear after preservation (unlike normal dendrobatid flash markings). Ventral surfaces are pale blue with some dark mottling but no pale dots. The vocalization of *A. isthminus* resembles calls of some South American species in being a train of “peeplike” notes, but there are fundamental interspecific differences in frequency modulation, note repetition rate, and call length.

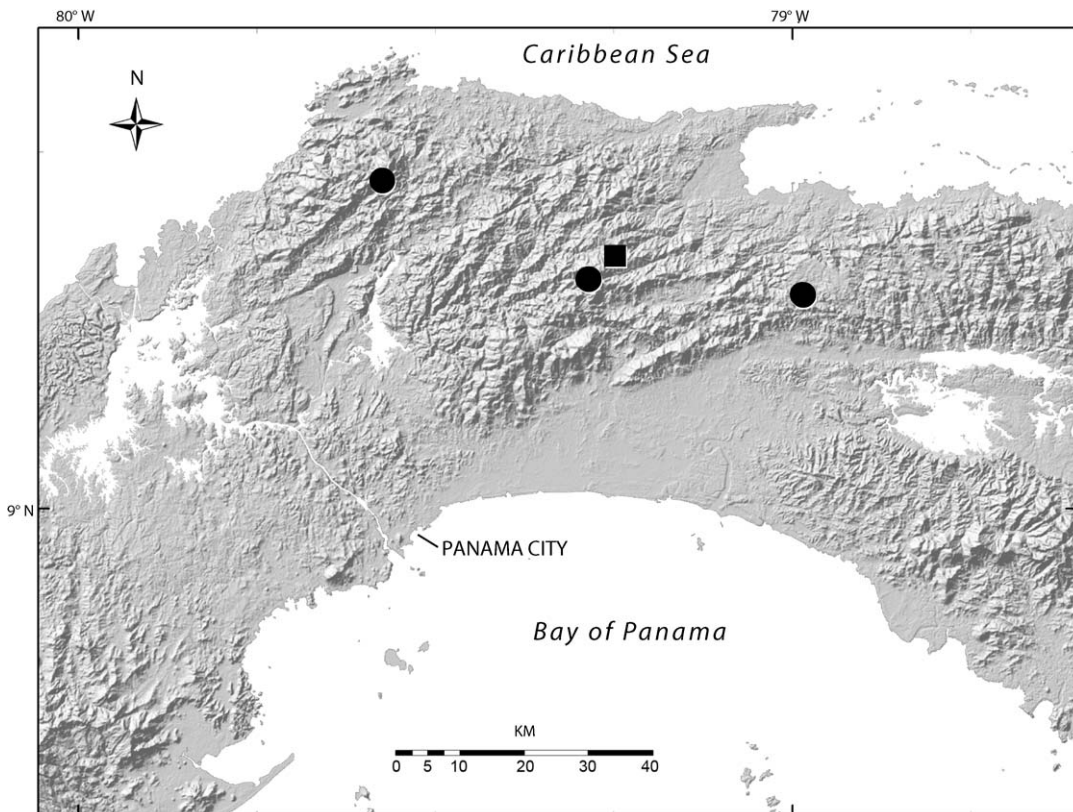
INTRODUCTION

The Isthmus of Panama harbors a rich fauna of dendrobatoid frogs that have both northern (Central American) and southern (South American) affinities. Endemism is high in western Panama among both elements of this fauna. In comparison, there have been relatively fewer speciation events among dendrobatoids in eastern Panama (although we are aware of unnamed cryptic species). In this paper we describe two species with South American affinities from the east-central part of the isthmus—in the low highlands east of the Panama Canal (map 1).

Myers et al. (2007: 14) commented that “It seems very odd that the low highlands northeast of Panama City have never received a widely accepted map name (usually no name is given, although ‘Sierra Maestra’ has been shown for part).” The names used in the herpetological literature (Pequeni-Esperanza Ridge, Piedras-Pacora Ridge, and Serranía Piedras-Pacora) are descriptive only of the southern parts of this uplift, much of which is drained by headwaters of the Río Chagres and also included in the Chagres National Park. This protected watershed is essential for operating the locks that raise and lower ships for passage through the Panama Canal. We propose the name **Chagres Highlands** for this physiographic entity, although some of its small rivers drain directly north to the Caribbean Sea or south to the Bay of Panama. The relatively broad expanse of the Chagres Highlands is geologically complex (Montes et al., 2012). It is abutted immediately on the east by the Serranía de San Blas—a narrow, broken range that carries the continental divide southward to the Serranía del Darién on the Colombian border. The Chagres Highlands may be a lower montane forest refuge for some rare amphibians and reptiles (see Discussion).

The first species described in this paper was discovered in 1974 by Catherine A. Toft. She collected a specimen from near the El Llano–Cartí Road, which crosses the low divide between the Chagres Highlands and the Serranía de San Blas (see easternmost symbol in map 1). The next specimens were not collected until 1997, when Ibáñez and Jaramillo discovered specimens at widely spaced localities in the Chagres Highlands (map 1).

Toft’s specimen was identified by Myers (1991) as *Colostethus chocoensis* (Boulenger), a species then known only from its type locality in Pacific western Colombia. Myers also tentatively extended the range of *C. chocoensis* south into Ecuador. Later, however, discovery of the “median lingual process” in New World dendrobatoids revealed that this curious structure is



MAP 1. Central Panama, showing locality records for two new species of *Anomaloglossus* in the Chagres Highlands. Black square, *A. astralogaster*. Black circles, *A. isthminus* (middle circle is the type locality). The Chagres Highlands comprise the upland northeastward of Panama City—between the Panama Canal (visible left of center) and the Serranía de San Blas (to the right of the easternmost *A. isthminus* locality).

lacking in “*Colostethus*” (now *Hyloxalus*) *chocoensis*, but that it is present in the Ecuadorian frogs (Grant et al., 1997: 24, fn. 13) and also in Toft’s Panamanian specimen (this paper). The systematics of “*Colostethus*” sensu lato had seemed nearly intractable, but phylogenetic analyses of DNA sequences and morphological and behavioral characters recovered monophyletic groupings, and the lingual process provided a morphological synapomorphy for the new genus *Anomaloglossus* (Grant et al., 2006: 158). The Ecuadorian frogs allocated by Myers to *chocoensis* were named *Anomaloglossus confusus* (Myers and Grant, 2009) and the Panamanian frogs are treated in this paper.

The first species of *Anomaloglossus* to be named is the one collected by Toft, Ibáñez, and Jaramillo, as mentioned above. To our surprise, however, a second new species of *Anomaloglossus* also occurs in the Chagres Highlands. It was collected during an unpublished biological survey (Roldán, 1985). This second species is known only from a single specimen, and it has a unique ventral pattern of pale chromatophore-like (glandular?) dots that we do not recall seeing in any other frog.

The type localities for the two new species are on Cerro Brewster, but on different sides of the political division between Provincia de Panamá and Comarca Guna Yala.⁵

METHODS: Measurements of specimens, hind-foot webbing formulae, and analysis of vocalizations follow the methods most recently discussed in Myers and Donnelly (2008: 12–13). Ocular-micrometer measurements labeled “sagittal” (from tip to snout to center of naris or to angle of jaw) are made in the plane parallel to the median or sagittal plane of the body.

Coordinates at the type locality of *Anomaloglossus isthminus* were determined by a hand-held GPS satellite receiver in 2009, after military restrictions had been lifted. (Prior to 2000, the point-position accuracy of commercially available GPS devices was limited to about 100 m). Coordinates for Cerro Bruja (a paratype locality) were taken in 1997 and are believed to be reasonably accurate because the reading coincided with map topography.

Coordinates for the type locality of *Anomaloglossus astralogaster* are estimates based on information supplied by the collector, Jorge Roldán H. The datum is WGS84 for all coordinates in this paper.

The locality map is based on a digital elevation model generated from the SRTM (Shuttle Radar Topography Mission) prepared by NASA and NGA (National Geospatial Intelligence Agency).

Anomaloglossus isthminus, new species

Figures 1A–D, 2–8; map 1

Colostethus chocoensis (Boulenger): Myers, 1991 (part: the single Panamanian specimen, KU 172790; figs. 3C, D, 4, 8D). Grant et al., 1997: 24, fn. 13 (part: only KU 172790; see Remarks).

HOLOTYPE: MVUP 2345 (originally CH 4568), an adult male from forest stream at headwaters of Río Piedras, Cerro Brewster, 810 m elevation, Provincia de Panamá (9°19'17" N, 79°17'10" W), collected by César A. Jaramillo, February 24, 1997.

PARATOPOTYPES (3): CH 4566, a juvenile female from forest stream, collected by César A. Jaramillo, February 24, 1997. CH 4552 and 4557 (=AMNH A-187134), adult males from forest stream, collected by César A. Jaramillo, February 25, 1997.

PARATYPES (2): CH 4512, an adult female from forest stream at headwaters of Río Piedras, SSW slope of Cerro Bruja, 720 m elevation, Provincia de Colón (9°27'35" N, 79°34'29" W), collected by Roberto Ibáñez, January 25, 1997. KU 172790, an adult male from forest stream west and down slope (150 m elev.) from km 11.7 (300 m) on road from El Llano to Cartí, Provincia de Panamá (approximately 9°18' N, 78°59' W), collected by Catherine A. Toft, July 1974).

⁵ This *Comarca* was shown on 20th century maps as the *Comarca de San Blas*, but it was changed to the “*Comarca Kuna Yala*” in the late 1990s. Apparently the letter “K” was officially removed from the Guna alphabet and in 2010 the name was again changed, to “*Comarca Guna Yala*” (or “*Gunayala*”). (See *Ley fundamental de la Comarca Gunayala* available through <http://www.congresogeneralkuna.com> [accessed July 19, 2012]). See also Price (2005: 176). The word *Kuna* (or *Cuna*) is in wide usage, so this is a major name change for this *comarca*, although borders are only slightly affected. But possible elevation to complete provincial status for other *comarcas indígenas* have profoundly changed the map of Panama, particularly as regards the provinces of Darién, Bocas del Toro, and Chiriquí.

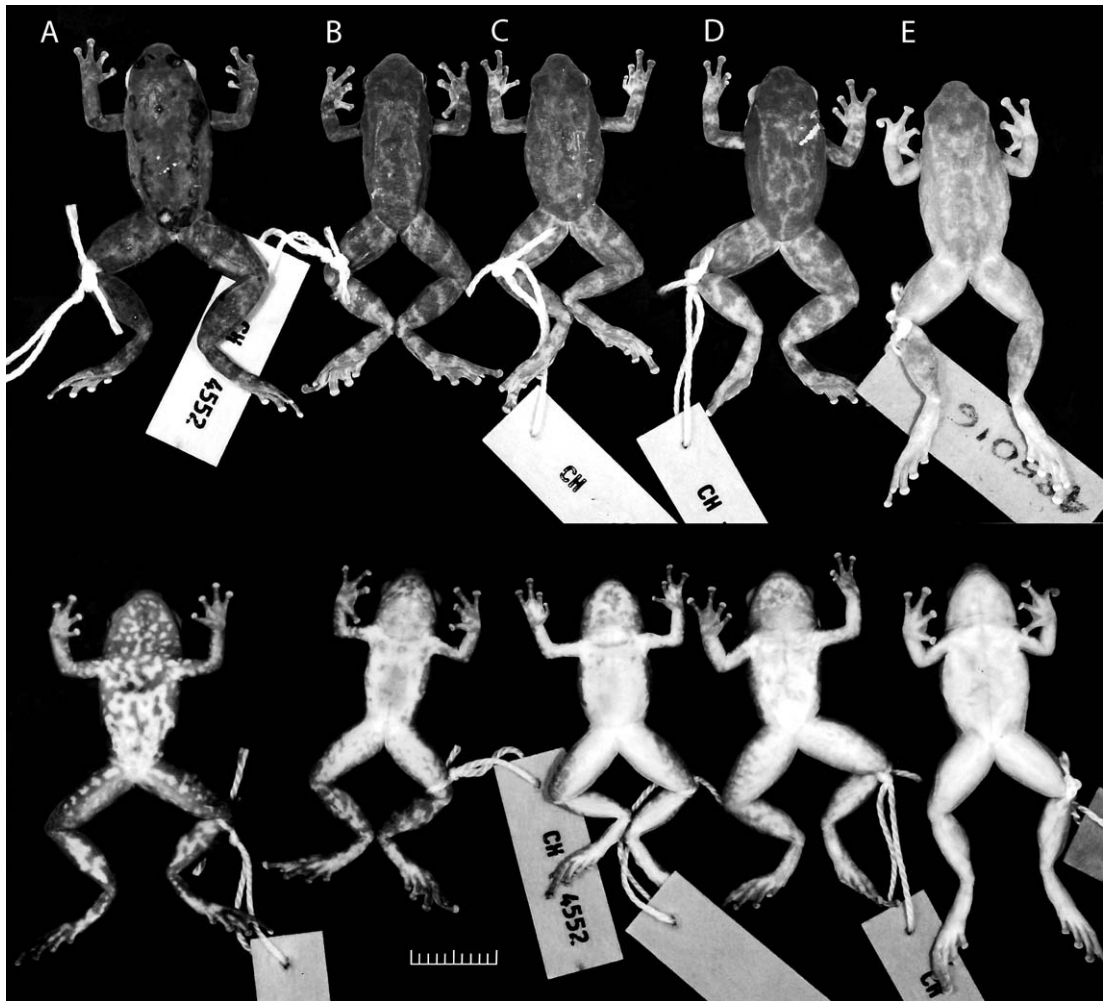


FIG. 1. Two Panamanian species of *Anomaloglossus* in dorsal and ventral views. A–D: *Anomaloglossus isthminus*, new species (left to right: CH 4512 ♀, 4552 ♂, 4557 ♂ [AMNH A-187134], MVUP 2345 ♂). E: *Anomaloglossus astralogaster*, new species (MVUP 2346 ♀). Scale = 10 mm.

ETYMOLOGY: The specific name is derived from Latin *isthmus* (< Greek *isthmos*) + *-inus* (*-a*, *-um*), an adjective-forming suffix meaning “belonging to,” in reference to the Isthmus of Panama.

DIAGNOSIS: A low median lingual process (fig. 2) or median pit (similar to fig. 11) distinguishes *Anomaloglossus isthminus* from all other named Central American frogs except *A. astralogaster*, which is differentiated by a punctate ventral pattern of discrete pale spots (see fig. 10). *A. isthminus* seems related to an unnamed species from the Colombian side of Cerro Tacarcuna (Grant et al., 2011). Based solely on a few color photographs, the Tacarcuna species differs from *A. isthminus* in having weak indications of a pale dorsolateral line and pale spotted, lighter sides; the lateral spots are aligned as a broken, oblique lateral stripe extending about halfway along the sides; the blue ventral surfaces with variable dark markings are very similar to *A. isthminus*.

MEASUREMENTS (IN MM) OF HOLOTYPE:

The specimen is an adult male (fig. 3) with open vocal slits. Length from snout to vent 20.6; tibia length between heel and outer surface of flexed knee 10.3; greatest width of body 9.5; greatest head width between angles of jaws and width between outer edges of upper eyelids 8.1 and 6.8, respectively; approximate width of interorbital area 3.5; head length (sagittal) from tip of snout to angle of jaw 5.6; tip of snout to center of naris (sagittal) 1.3; center of naris to anterior edge of eye 1.5; distance between centers of nares 2.9; eye length from anterior to posterior edge 3.3; tympanum nearly concealed; hand length from proximal edge of large medial palmar tubercle to tip of longest (third) finger 5.5; width of disc of third finger (and width of penultimate phalanx below disc) 1.0 (0.6); width of discs (and penultimate phalanges below discs) of third and fourth toes 1.1 (0.7) and 1.0 (0.7), respectively.



FIG. 2. The median lingual process (arrow) in *Anomaloglossus isthminus*, new species (MVUP 2345 holotype), approximately $\times 13$.

DESCRIPTION

The type series comprises six specimens from three localities in east-central Panama. Four adult males, one adult female, and one juvenile female (in poor condition) are included. Measurements and proportions given in the following description are for the five adults.

MORPHOLOGY: Adult males 19.4–21.3 mm SVL ($n = 4$, $\bar{x} = 20.33 \pm 0.41$ mm); testes unpigmented, white, large (~1.8–2.2 mm long), roughly one-half of kidney length. Adult female (CH 4512) 22.6 mm SVL, with large, convoluted oviducts and large brown ova. A low median lingual process (fig. 2) discernible on tongue except that it is seemingly retracted and concealed in a pit in CH 4552. See Discussion.

Skin in preservative smoothly rugose to faintly granular dorsally, smooth ventrally; no posttricial or cloacal tubercles. Greatest head width (between angles of jaws) 35%–39% of SVL. Snout sloping, acutely rounded (nearly pointed) in profile, broadly rounded to nearly truncate in dorsal and ventral view. Nares visible from in front, barely visible from above or below. Canthus rostralis rounded to weakly angulate; loreal region slightly concave, sloping slightly outward to lip. Interorbital region not well defined but nonetheless noticeably wider than upper eyelid. Length of snout in lateral view much shorter (64%–79%) than eye length; center naris to edge of eye 50%–64% of eye length. Tympanic annulus and membrane virtually concealed in a few specimens; otherwise

weakly indicated antero-ventrally and concealed by diffuse supratympanic bulge posterodorsally; tympanum small, its estimated diameter less than one-half of eye length. Teeth present on maxilla.

Hand (fig. 4) relatively small, its length in four adult males 26%–27% of SVL, 68%–74% of greatest head width; smaller hand in one adult female 23% SVL, 59% head width. Relative lengths of appressed fingers III > IV \geq II > I; tip of finger I either reaching or failing to reach disc of finger II; finger III not swollen. Discs of all fingers moderately expanded; third finger disc 1.4–1.7 times wider than distal end of

adjacent phalanx. Base of palm with a large, irregularly rounded, median metacarpal tubercle, a smaller elliptical inner metacarpal tubercle on base of first finger; one to three subarticular tubercles (one each on fingers I, II; two or three on fingers III, IV; an inconspicuous small, distal third subarticular tubercle sometimes distinguishable on fingers III and IV); all tubercles low, with slightly rounded surfaces. Fringes along sides of fingers weakly developed (virtually absent); proximal part of fringe on median side of first finger extending faintly to inner metacarpal tubercle; fringe on lateral side of fourth finger faintly continuous with a weak outer metacarpal fold that extends to the large palmar tubercle.

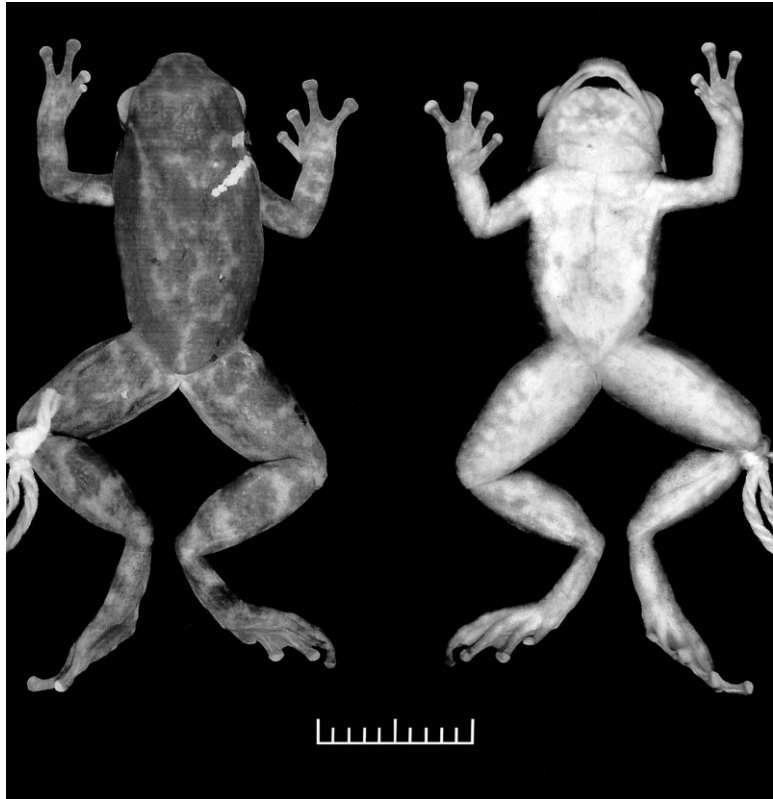


FIG. 3. *Anomaloglossus isthminus*, new species. Dorsal and ventral views of adult male holotype (MVUP 2345). Scale = 10 mm.

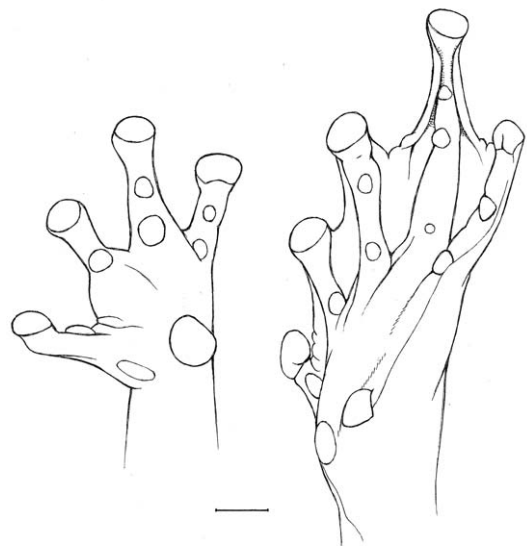


FIG. 4. Left hand and left foot of *Anomaloglossus isthminus*, new species (CH 4512, adult female paratype). Scale line = 1 mm.

Hind limbs relatively long, with heel of forward-pressed limb reaching to snout tip or between eye and snout tip; tibia 48%–52% of SVL. Relative lengths of appressed toes $IV > V \approx III > II > I$; first toe reaching middle of subarticular tubercle of second. Toe discs noticeably expanded, those on third and fourth toes 1.3–1.8 times wider than adjacent phalanges. Feet “webbed” to base of each toe disc, although the web is distally narrowed to a fringe on medial sides of toes II and III and on both sides of toe IV, yielding an approximate webbing formula of **I 1–2 II 1–2 III 1–2 IV 2–1 V** (fig. 4). The fringes fold downward along each side of toe IV, forming “folded flaplike fringes.”⁶ A well-developed fringe along the outer free edges of toes I and V. One to three nonprotuberant subarticular tubercles; a small round to oval outer metatarsal tubercle and a slightly longer elliptical inner metatarsal tubercle. An oblique tarsal fold extending proximolateral on distal half of tarsus is continuous with fringe on free edge of first toe; tarsal fold varying from a weak ridge to a strong keel, lacking tubercle or pronounced elevation at its proximal end.

COLOR IN LIFE: Based on a few color photographs and the collectors’ color notes abstracted below, the dorsal body varies from brown with irregular dark brown or cream blotching to blackish-brown with greenish-gold reticulum. The aforesaid “greenish” dorsal reticulum—documented in a color photo of the holotype—is more bronzy in another view of the same specimen (fig. 5). Sides brown without conspicuous pale spots or oblique lateral stripe. A narrow, sometimes broken postocular line from below eye to arm insertion varies from “blue-gold” to bronze (fig. 5).

There are either bright yellow or pale blue-gold marks atop base of the upper arm and atop thigh near groin (these markings appear very pale yellowish in color photos of the holotype). Venter light blue (fig. 6), with blackish reticulations on throat and scattered over abdominal area and limbs as described for the adult female below.]

CH 4512 (adult female): Dorsum brown with some irregular darker blotches. A bright yellow spot in [near] the groin and at the dorsal insertion of upper arm. Venter light blue with a black reticulum. This black reticulum extends to the belly, throat, arms and legs.

CH 4552 (adult male): Iris dark brown. Two light blue-gold spots behind the eye, towards the insertion of arm. Dorsum brown with some irregular cream blotches. Anterior area of throat light blue with brown blotches, rest of throat brown. Chest, belly and anterior ventral surface of thighs light blue. Posterior ventral surface of thighs brown. Concealed surfaces of shanks and feet light blue. Dorsal surface of hind legs with light and dark brown bars. A light blue-gold spot on anterior portion of hind leg near the groin and at the dorsal insertion of upper arm.

CH 4557 (adult male): A fine light blue-gold line posterior to eye. Dorsum brown with some irregular black blotches. Throat and belly light blue. The throat with a central brown blotch. Dorsal surface of thighs with dark brown and black bars. Anterior ventral surface of thighs light blue. A light blue-gold spot on anterosuperior portion of thigh near the groin and at the dorsal insertion of upper arm.

⁶ As defined by Myers and Donnelly (2008: 42).



FIG. 5. *Anomaloglossus isthminus*, new species. The adult male holotype. in life (MVUP 2345, 20.6 mm SVL) (photographed by Marcos Guerra at Smithsonian Tropical Research Institute).

CH 4566 (juvenile female): Similar in color to CH 4557. Venter light blue with small brown blotches in the throat.

MVUP 2345 (CH 4568, adult male): Iris light brown. A fine light blue-gold line posterior to eye, towards the insertion of arm. Dorsum dark brown (almost black) with a greenish gold reticulum. Throat brown with light blue blotches on anterior area of throat. Belly and anterior ventral surface of thighs light blue. Dorsal surface of thighs with brown and golden brown bars. Concealed surfaces of shanks light blue. A light blue-gold spot at the base (anterosuperior portion) of the hind leg and at the dorsal insertion of upper arm. Pericloacal area orange.

KU 172790 (adult male): "chocolate brown above, with a yellow flash mark atop base of upper arm, and with a tinge of metallic blue on the venter" as given in Myers (1991: 5).



FIG. 6. *Anomaloglossus isthminus*, new species. Ventral view of the adult male holotype in life (photographed by Marcos Guerra at Smithsonian Tropical Research Institute).

COLOR PATTERN IN PRESERVATIVE (figs. 1A–D, 3): Dorsum pale to light brown, with irregular spots and blotches of dark brown. Loreal region and upper lip suffused with brown. A distinct to indistinct, narrow whitish postocular line, which starts below lower rear edge of eye and extends obliquely (nearly horizontally in one) between tympanic area and corner of mouth to the arm. Flanks brown, lacking pale stripes; axilla and groin either brown or whitish, without pale flash marks. Limbs irregularly banded with dark and light brown; fingers I and II partly whitish. Rear of thighs brown without definite pattern. Ventral surfaces whitish, with brown blotching or brown reticulum under head, this pattern extending weakly to strongly onto chest; some inconspicuous small suffusions of pale brown on belly. Palms and soles brown.

The golden marks atop the base of the upper arm and atop the thigh near the groin are essentially lost in preservative (fig. 1; Myers, 1991: fig. 3C), although a few specimens retain diffuse pale yellowish spots on the upper arm above axilla (fig. 1B, 1D). This is in contrast to many dendrobatoids that have bright axillary and/or inguinal flash marks that remain conspicuous even in preservative.

VOCALIZATION

Anomaloglossus isthminus is diurnal and has been heard calling only by day. Tape recordings were made by Jaramillo along a headwater branch of the Río Piedras at the type locality, at a daytime air temperature of 21° C on February 25, 1997. Part of the 14-minute tape is of a specimen of *A. isthminus* calling from a rock in the stream, with consequential loud background noise of flowing water; some other calling individuals were concealed. The 1–14 note vocalizations of another dendrobatoid, *Colostethus pratti*, also can be heard on the first part of

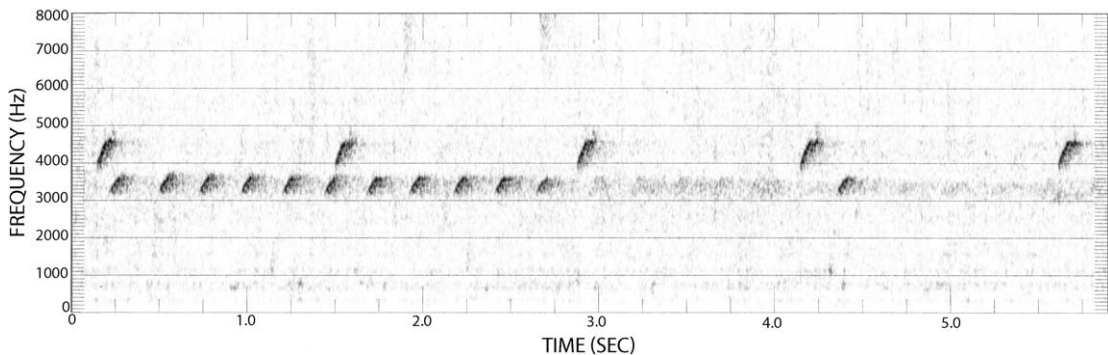


FIG. 7. Vocalizations of sympatric dendrobatoid frogs (narrow band, 63 Hz). Frequency above 4000 Hz: five well-spaced notes of *Anomaloglossus isthminus*, new species. Frequency below 4000 Hz: a complete call (11 notes + 1 single note) of *Colostethus pratti*. Blurring of the signals is caused by loud background noise of running water. (Copy of tape on AMNH herpetology reel 292; other dendrobatoids recorded in background of this tape are *Allobates talamancae* and *Silverstoneia nubicola*).

this tape, including an individual calling in close proximity to *A. isthminus* (fig. 7). Other dendrobatoids recorded in the background of this tape were *Allobates talamancae* and *Silverstoneia nubicola*.

A better recording (without background interference) of *Anomaloglossus isthminus* was obtained nearby from an individual (CH 452) calling from concealment among rocks or dead leaves. Like earlier calls on the tape, its call is comprised of a train of similarly well-spaced notes given at a frequency mainly between 4 and 5 kHz. The following description and figure 8 is based on this specimen.

This call is a long train (> 1 min) of single, weakly pulsatile notes heard as loud peeps given at an average intracall rate of 1.3 notes/sec. Spacing between notes is somewhat variable; inter-note interval in one 29-sec sample ranges from 0.94 to 1.4 sec (\bar{x} = 1.386, SD = 0.158, n = 22). Note duration is 0.08–0.09 sec as measured from waveforms, with each note comprised of three incompletely separated pulses. Narrow-band analysis shows the notes to be narrowly tuned and frequency modulated, with frequency rising sharply from about 3700–3900 Hz to 4900 Hz.

The vocalizations of several South American species of *Anomaloglossus* have been described and illustrated: *A. atopoglossus* (Colombia; Grant et al., 1997), *A. tamacuarensis* (Venezuela; Myers and Donnelly, 1997), and *A. tepuyensis* (Venezuela; Myers and Donnelly, 2008). Except for producing trains of notes sounding like “peeps” or “cheeps,” there is little resemblance between calls of these species and that of *A. isthminus*. The call of *Anomaloglossus atopoglossus* comprises only 12–14 notes that individually ascend and then slightly decline in frequency throughout the short (~ 1 sec) train; *A. tamacuarensis* has a long (≥ 1 min) train of double notes given at constant frequency; *A. tepuyensis* has a short (< 5 sec) train of rapidly given notes with little frequency modulation. *A. isthminus* produces a long train of notes (like *A. tamacuarensis*) that differ from the other calls in being slowly produced and strongly modulated in frequency. There also are pronounced differences among the species in carrier frequency and pulsation.

REMARKS: All specimens of *Anomaloglossus isthminus* were found along the edges of forest streams. The species was found syntopically with the more abundant *Colostethus panamansis*

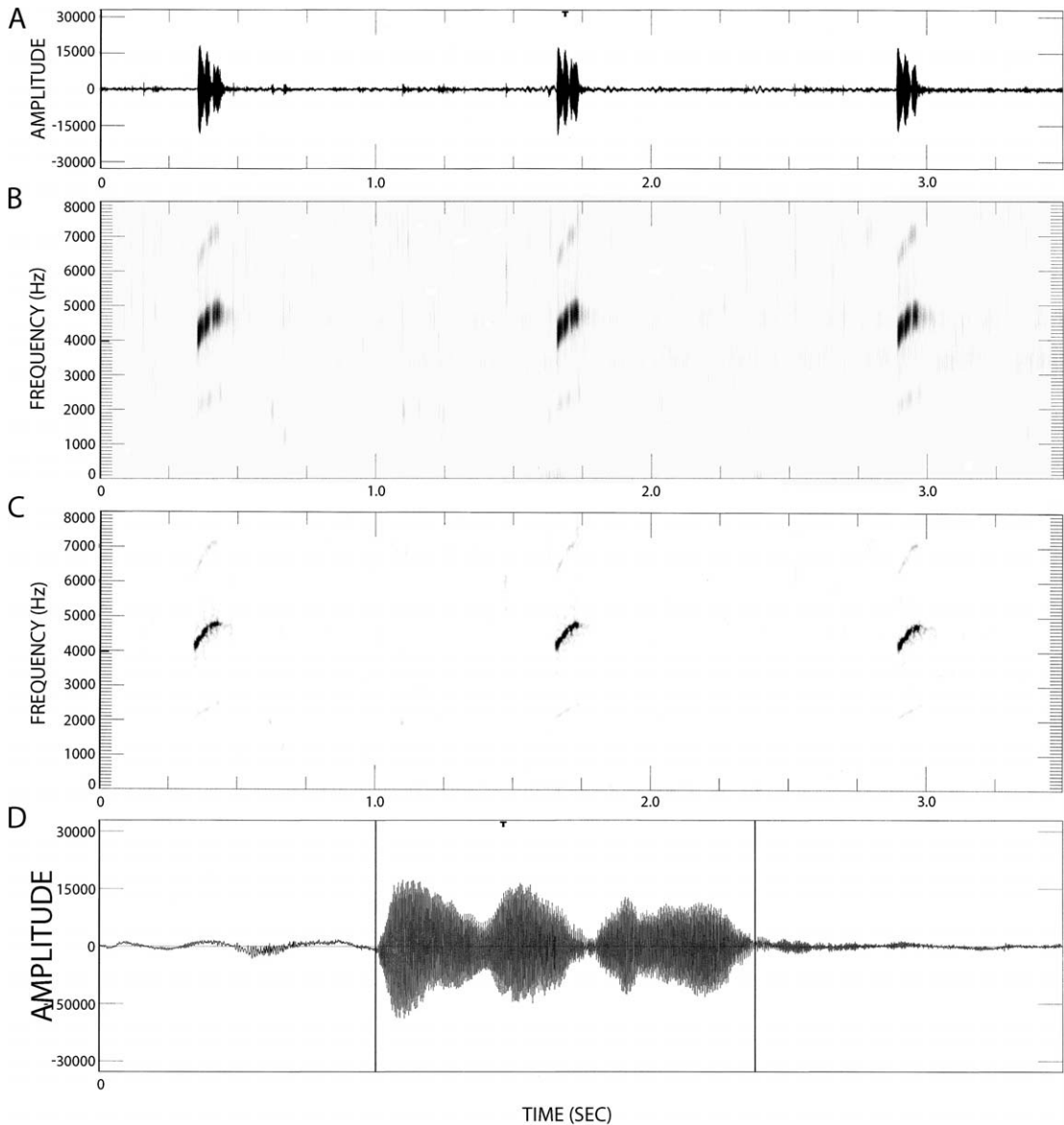


FIG. 8. Vocalization of *Anomaloglossus isthminus*, new species. Three notes from a sequence of 64 notes in an 80-sec call. **A:** Waveforms. **B:** Wide-band (323 Hz) spectrogram. **C:** Narrow-band (63 Hz) spectrogram. **D:** Expanded waveform of tagged (middle) note from panel A, showing three distinct pulses. Time between cursors = 0.083 sec. Recording of paratopotype CH 4552, recorded by day at type locality, February 25, 1997; air temperature 21°C. (Copy of tape on AMNH herpetology reel 292).

at Cerro Brewster and Cerro Bruja. Based on observations at Cerro Brewster, however, the two species tend to occupy different sections of the streams.

In addition to the paratopotypes collected and recorded February 24–25, 1997, *A. isthminus* was heard calling but was not collected at one other stream near the type locality. The general area of the type locality subsequently was searched by Ibáñez on November 11–12,

2007, November 16–18, 2009, and December 10–14, 2009, but the species was neither seen nor heard during those times. During February 26–March 3, 2008, however, a single individual was caught in the stream where the holotype had been found (Edgardo J. Griffith, personal commun.). The species seems to be very rare, or at least extremely secretive when not breeding.

A paratypic specimen of *Anomaloglossus isthminus* was reported as lacking a median lingual process (Grant et al., 1997: 24, fn. 13, re KU 172790). A low, inconspicuous process, however, is present in the specimen (Linda Trueb, personal commun.).

***Anomaloglossus astralogaster*, new species**

Figures 1E, 9–11; map 1

HOLOTYPE: MVUP 2346 (original no. 485016), an adult female from Cerro Brewster, 700–900 m, Comarca Guna Yala (approximately 9°21' N, 79°15' W). Collected by Jorge Roldán H., April 16–19, 1985.

ETYMOLOGY: The specific name is a noun in apposition derived from Greek *astralos* (speckled, star spotted) + *gaster* (belly), in reference to the distinctive ventral pattern.

DIAGNOSIS: The pale-dotted ventral pattern of round chromatophores or small flat glands (see fig.10 and fn. 7) distinguishes *Anomaloglossus astralogaster* from other known species of the genus. Under magnification, the pale dots and flecking on the venters of some other species are seen to be irregularly shaped pale areas of ground color (not discrete structures) showing through a dense reticulum of melanophores (e.g., Myers and Donnelly, 2008: 35, fig. 16).

MEASUREMENTS (IN MM) OF HOLOTYPE: Length from snout to vent 22.2; tibia length between heel and outer surface of flexed knee 10.1; greatest width of body 10.2; head width between angles of jaws, and between outer edges upper eyelids, 8.1, 6.5 respectively; approximate width of inter-orbital area 2.8; head length (sagittal) from tip of snout to angle of jaw 5.0; tip of snout to center of naris (sagittal) 0.3; center of naris to anterior edge of eye 1.9; distance between centers of nares 3.1; eye length from anterior to posterior edge 3.3; horizontal diameter of tympanum about 1 (posteriorly concealed); corner of mouth to lower edge of tympanic ring 0.9; hand length from proximal edge of large medial palmar tubercle to tip of longest (third) finger 6.0; width of disc of third finger (and width of penultimate phalanx below disc) 1.3 (0.7); width of discs (and penultimate phalanges below discs) of third and fourth toes identically 1.2 (0.8).

DESCRIPTION OF HOLOTYPE

The unique specimen is somewhat faded (fig. 1E) but otherwise in fair condition. However, there are slight preservation distortions in the extremities, especially puffiness in the hands; basic descriptions are adequate, but drawings of the hand and foot were not made.

MORPHOLOGY: An adult female with large convoluted oviducts and large pigmented (pale brown) ova about 2 mm in diameter. Tongue with pronounced pit (fig. 11) that presumably conceals a short retractable median lingual process. See Discussion.

Skin in preservative smooth dorsally and ventrally; no postrictal or cloacal tubercles. Greatest head width (between angles of jaws) 36% of SVL. Snout sloping, acutely rounded

(nearly pointed) in profile, broadly rounded in dorsal and ventral view. Nares visible from in front and from below, not visible from above. Canthus rostralis weakly angulate; loreal region nearly vertical, sloping slightly outward to lip. Interorbital region noticeably wider than upper eyelid. Length of snout in lateral view much shorter (63%) than eye length; center of naris to edge of eye 57% of eye length. Tympanic annulus and membrane visible anteriorly, but concealed posteriorly (concealed by diffuse supratympanic bulge posterodorsally and by skin posteroventrally; tympanum small, its estimated diameter much less than one-half of eye length. Teeth present on maxilla.

Hand relatively small, its length in adult female 27% of SVL, 74% of greatest head width. Relative lengths of appressed fingers III > IV > II > I; tip of finger I reaching disc of finger II; finger III not swollen. Discs of all fingers moderately expanded; third finger disc 1.8 times wider than distal end of adjacent phalanx. Base of palm with a large rounded median metacarpal tubercle; a smaller elliptical inner metacarpal tubercle on base of first finger; one or two subarticular tubercles (one each on fingers I, II; two on fingers III, IV); all tubercles low, with slightly rounded surfaces. Fringes along sides of fingers weakly developed; proximal part of fringe on median side of first finger extending faintly to inner metacarpal tubercle; fringe on lateral side of fourth finger faintly continuous with a weak outer metacarpal fold that extends to the large palmar tubercle.

Hind limbs moderate, with heel of forward-pressed limb failing to reach eye; tibia 44% of SVL. Relative lengths of appressed toes IV > V \approx III > II > I; first toe reaching middle of subarticular tubercle of second. Toe discs noticeably expanded, those on third and fourth toes 1.5 times wider than adjacent phalanges. Feet "webbed" to base of each toe disc, although the web is distally

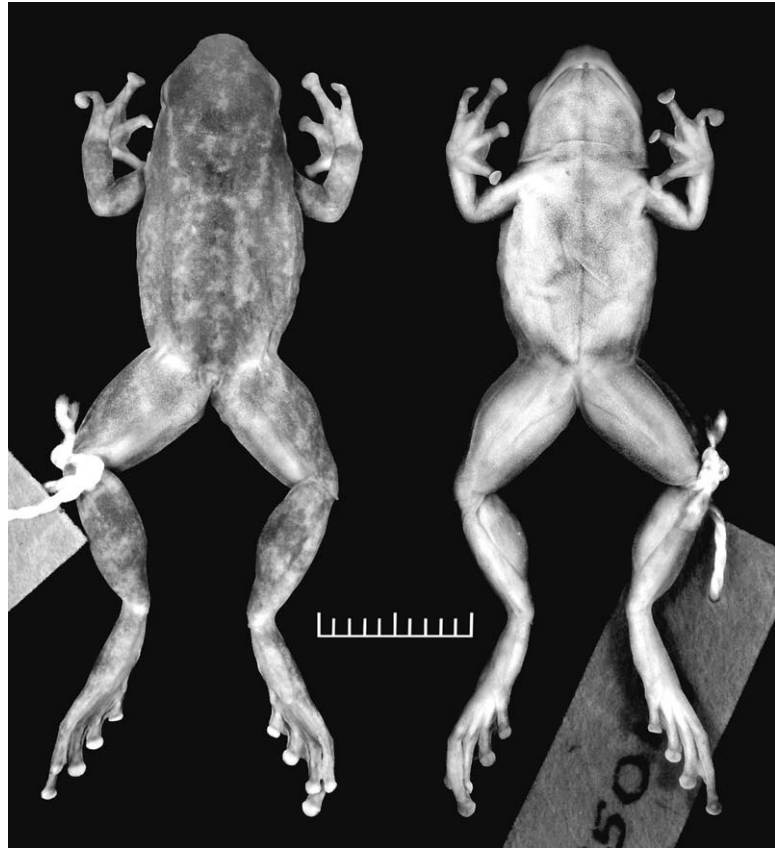


FIG. 9. *Anomaloglossus astralogaster*, new species. Dorsal and ventral views of adult female holotype (MVUP 2346). Scale = 10 mm. (See figure 10 for magnified view of ventral pattern.)

narrowed to a fringe on medial sides of toes II and III and on both sides of toe IV, yielding an approximate webbing formula of I 1–1½ II 1–2 III 1–2 IV 1½–1 V. The fringes fold downward along each side of toe IV, forming “folded flap-like fringes.” A downward-folded fringe along the outer free edges of toes I and V. One to three nonprotuberant subarticular tubercles; a small round protuberant outer metatarsal tubercle and a slightly longer elliptical inner metatarsal tubercle. An oblique tarsal fold extending proximolaterad on distal half of tarsus is continuous with fringe on free edge of first toe; tarsal fold a strong ridge, lacking tubercle or pronounced elevation at its proximal end.

COLOR PATTERN IN PRESERVATIVE (figs. 1E, 9–10): Dorsum light yellowish brown with ill-defined darker brown markings, including an interorbital blotch, a V-shaped scapular blotch, an elongate vertebral blotch, and narrow dorsolateral stripes. Loreal region and upper lip unmarked pale brown. A brown postocular blotch starts narrowly at upper edge of eye and widens posteriorly; the upper edge of this marking is posteriorly confluent with the brown dorsolateral stripe; the lower edge extends obliquely to the shoulder across the upper edge of the tympanum; the lower edge of the brown postocular marking forms a dark brown streak on the left side of the head, whereas on the right side it appears as a distinct, narrow dark stripe from eye to shoulder. Flanks brown, lacking pale stripes; axilla and groin lack defined flash marks (in life, diffuse spots conceivably present in axilla and groin, where skin is now transparent). Limbs indistinctly banded with dark and light brown. Rear of thighs pale brown without definite pattern.

Skin of ventral surfaces overall translucent (musculature visible) and covered with discrete whitish dots (either chromatophores or small glands $\leq 0.1 \text{ mm}^2$) that are dense on



FIG. 10. *Anomaloglossus astralogaster*, new species. Enlarged view of holotype showing diagnostic pale-dotted ventral pattern of discrete round chromatophores (or small glands?), $\times 6.2$.

⁷ Despite their relatively large size, we tentatively called these “chromatophores” because they are not visibly raised above the skin surface and because there is no appearance of glandular structure at $\times 50$ magnification. However, the edges of some individual dots can be “felt” with the tip of a fine (0.1 mm diameter) teasing needle. Histological examination is needed for final determination of these curious structures.

throat and belly and less dense under limbs (fig. 10). Dark pigment lacking except for tiny punctate melanophores present sparingly and visible (at high magnification) on tip of chin, throat, and chest. Palms essentially unpigmented, soles pale brown.

PROVENANCE OF THE HOLOTYPE

The unique specimen of *Anomaloglossus astralogaster* unfortunately lacks color notes and specific collecting data. It was collected during a series of biological surveys in what was designated “La Reserva Kuna Yala,”⁸ located in the western part of the Comarca Guna Yala (formerly shown on maps as “Comarca de San Blas” and, later, as “Comarca Kuna Yala”). Jorge Roldán H. was in charge of the herpetological surveys; other people including park guards assisted in collecting. Roldán wrote three unpublished reports in 1984 and 1985, but the last one sheds light on where the specimen was found. Roldán (1985 MS) listed a “*Colostethus* [sic] sp.” for Cerro Brewster, Guna Yala, from approximately 700 to 900 m in elevation. The other *Colostethus* listed for Cerro Brewster was *C. flotator* (now *Silverstoneia flotator*). Roldán’s several reports have all dendrobatoids identified to species except for the specimen of *Anomaloglossus astralogaster*; all are species that are clearly different from *A. astralogaster*.

Therefore, we accept Cerro Brewster, Comarca Guna Yala, as the type locality of *A. astralogaster*. Roldán’s trip to Cerro Brewster was carried out April 16–19, 1985. The locality is about 1 hr walk northeastward from the type locality of *Anomaloglossus isthminus*; Roldán approached the site by walking eastward from Altos de Pacora and passing the geodesic marker for Cerro Brewster (Roldán, personal commun.).

Cerro Brewster is located along a montane ridge in the Chagres Highlands that includes the type localities of both *Anomaloglossus isthminus* at 810 m elevation and *A. astralogaster* at

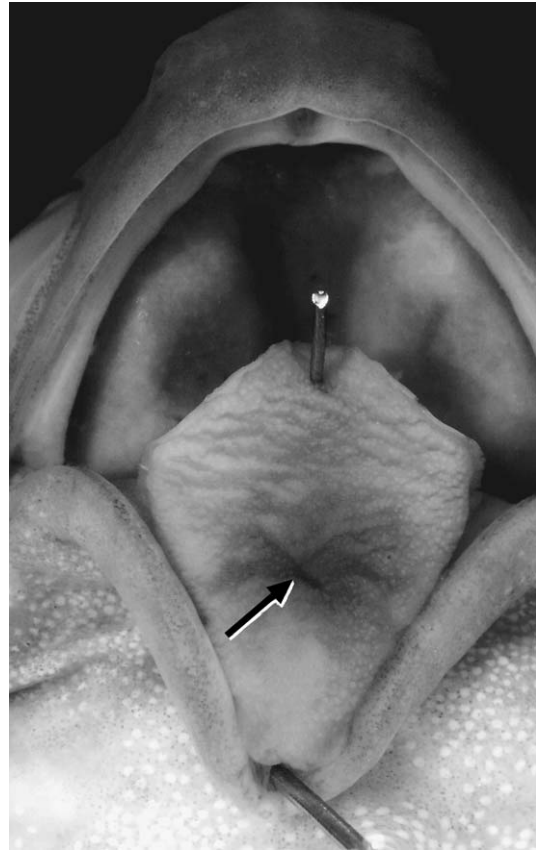


FIG. 11. *Anomaloglossus astralogaster*, new species. Tongue of holotype showing “pit” (arrow) that presumably conceals a retracted median lingual process (cf. fig. 2), approximately $\times 12$.

⁸ The approximate area of Reserva Guna Yala extends on the mainland from the western and southern limits of the Comarca Guna Yala to the Llano-Cartí Road (locality for the easternmost record of *A. isthminus*; see map 1). Currently, the reserve is recognized by the Autoridad Nacional del Ambiente de Panamá as part of a protected area, the “Área Silvestre Narganá.” The current protected area is more extensive, having been extended to the east, and is about three times the size of the initial reserve.

700–900 m (map 1). The type locality for *A. isthminus* lies in Provincia de Panamá, whereas the type locality for *A. astralogaster* is in Comarca Guna Yala.

DISCUSSION

Although the two new Panamanian species of *Anomaloglossus* are known only from the Chagres Highlands in east-central Panama, it cannot be safely concluded that they are endemic there. The best known part of these highlands is the Piedras-Pacora Ridge on the continental divide (Ibáñez et al., “1994” [1995]), which has been suggested as a “premontane forest refuge for some small part of the [herpeto]fauna that is barely surviving the climatic-vegetational vicissitudes of the Pleistocene” (Myers, 2003: 5). Indicator species more broadly include the frogs *Anomaloglossus astralogaster*, *A. isthminus*, and *Atelopus limosus*, as well as the very rare snakes *Atractus depressiocellus*, *A. imperfectus*, *Geophis bellus*, and *Rhadinaea sargenti*. But some other rare species in the Panamanian fauna have very fragmented or mosaic distributions, part of which includes the Chagres Highlands generally; examples include *Andinobates fulguritus*, *Anolis kunayalae*, *Coniophanes joanae*, *Geophis bracycephalus*, and *Dipsas nicholsi*. It is not possible to differentiate between endemism and range fragmentation based on a few records of rarely collected animals.

It is conceivable therefore that *Anomaloglossus* occurs more widely in Panama, possibly, for example, in fragmented pockets along the broken Serranía de San Blas and northern part of the Serranía del Darién, where collecting has been very sporadic. In any case, Panamanian *Anomaloglossus* clearly have South American affinities. The geographically closest congener is an unnamed species from the Colombian side of Cerro Tacarcuna, in the Serranía del Darién—some 60 km southeast of the nearest locality for *A. isthminus*. The Tacarcuna species lacks the peculiar ventral markings of *A. astralogaster* but is phenotypically similar to *A. isthminus* (see *isthminus* diagnosis). The other geographically closest relatives to Panamanian *Anomaloglossus* spp. are the trans-Andean *A. atopoglossus* (Grant, Humphrey, and Myers), *A. lacrimosus* (Myers), and *A. confusus* (Myers and Grant). These appear to form a clade phylogenetically distant from the 20-some species of cis-*Anomaloglossus* in northeastern South America (Grant et al., 2011).

The “median lingual process” (MLP) was found to be fairly widespread among Old World ranoids, but its discovery in South American dendrobatoids was a surprise. The surprise continues with a new finding that the MLP may have evolved twice in the Dendrobatoidea (Grant et al., 2011; unpublished), which may require erecting a new genus for trans-Andean and Panamanian “*Anomaloglossus*.”

Variation in the MLP is not well understood, particularly as regards the presence or absence of retractility of the process (discussions in Grant et al., 1997; 2006: 92–94). Compared with most other *Anomaloglossus*, the MLP is inconspicuous in *A. isthminus*. A short flattened or bumplike process is present in five of six *A. isthminus*, but the sixth specimen (CH 4552) seems to have only a pit; the unique specimen of *A. astralogaster* shows only a pit. It is assumed that a retractable MLP is present in all, but that, if not, the “lingual pit” is at least in some way

homologous. These seem to be the first records of lingual pits without evident MLP's in *Anomaloglossus*, although lingual pits apparently without processes are known in some Old World frogs and in South American *Dischidodactylus duidensis* (discussion in Grant et al., 1997: 17–19). In any case, lingual pits without processes are rare in *Anomaloglossus*.

ACKNOWLEDGMENTS

We thank William E. Duellman and Linda Trueb (KU) for lending the first known Panamanian specimen of *Anomaloglossus*, which was collected by Catherine A. Toft in July 1974. Myers thanks Toft for taking him to her approximate locality in 1976, when they unsuccessfully searched for additional material of this species (*Anomaloglossus isthminus* n. sp., reported as “*Colostethus chocoensis*” by Myers, 1991: 5–7). Later fieldwork leading to collection of the paratypes of *A. isthminus* by Ibáñez and Jaramillo was conducted during the Smithsonian Tropical Research Institute’s “Proyecto de Monitoreo de la Cuenca del Canal de Panamá,” supported by the United States Agency for International Development. Edgardo J. Griffith provided information on additional sightings of *A. isthminus*.

The holotype of *A. astralogaster* was collected during a biological survey of “La Reserva Kuna Yala” (Roldán, 1985). We thank Jorge Roldán H. for collecting the only known specimen of this species and for confirming its type locality.

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APPENDIX 1: MUSEUM ABBREVIATIONS

AMNH	American Museum of Natural History, New York
CH	Círculo Herpetológico de Panamá, Republic of Panama
KU	Museum of Natural History, University of Kansas, Lawrence
MVUP	Museo de Vertebrados de la Universidad de Panamá, Republic of Panama

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