On the distribution of the endemic Boettger’s Colombian Treefrog, *Dendropsophus columbianus* (Anura: Hylidae) with distribution extension in southwestern Colombia

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**Abstract.** We reviewed the distribution of *Dendropsophus columbianus* and introduced three new localities for the Andean region in Department of Cauca: i) the upper Patía River basin; ii) the western slopes of the Central Cordillera (Quintana, Popayán municipality); and iii) the western slopes of the Western Cordillera in El Tambo municipality, Colombia. The Patía River record extends its distribution 40 km south from previously known records and constitutes the lowest confirmed elevation known for the species (700 m a.s.l.). The Quintana record extends the upper high altitudinal distribution by 160 meters. Our records also extend the distribution of the species to two additional river basins (Patía and San Joaquín rivers). We also reviewed extra-distributional records outside the Andean region available from the literature from two localities (Quimarí and Guapi) in the Caribbean and Pacific regions of Colombia. Specimens from Quimarí were re-identified as *D. phlebodes*; and the specimens from Guapi belong to *D. columbianus* but the locality is likely erroneous. Using the validated localities, we built a distribution model corroborating its high association to Andean ecoregions in the Western and Central cordilleras of Colombia. The potential distribution of the species extends from Nariño to Antioquia following the Cauca River basin. Although the model shows that the presence of *D. columbianus* in Antioquia (north) and Nariño (south) is likely, the northern and southern boundaries of the species distribution is unclear due to the absence of records. Future expeditions are necessary to verify the limits of the species distribution.

**Keywords:** Boettger’s Colombian treefrog, Cauca, geographic distribution, Patía River

**Introduction**

The Boettger’s Colombian Treefrog, *Dendropsophus columbianus* (Boettger, 1892) (Anura: Hylidae) is a small anuran species (snout-vent length: 23-36 mm) distributed across the Colombian Andes between 950 and 2350 m a.s.l (Frost, 2016). It is common and considered endemic to the Cauca River basin, between the western slopes of the Central Cordillera and the eastern slopes of the Occidental (Western) Cordillera, in the departments of Antioquia, Cauca, Caldas, Quindío, Risaralda, and Valle del Cauca (Duellman and Trueb, 1983; Kaplan, 1997; Acosta-Galvis, 2000; Bolivar and Renjifo, 2004; Blandón-Marin, 2005; Agudelo-Valderrama et al., 2014). Three known records outside of this range (Guerrero-Vargas et al., 2007) were not included in recent updates of the distribution of the species (Agudelo-Valderrama et al., 2014). These are from (1) Quimari, Córdoba, in the Caribbean region, (2) Guapi, Cauca, in the Pacific region, and (3) the Finca Hawai, Patía River basin, Cauca, in an inter-Andean valley.

The voucher specimens for these records are deposited at the Museo de Historia Natural de la Universidad del

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Table 1. Measurements (in mm) of *Dendropsophus columbianus* collected at different localities in southwestern Colombia (See appendix 2 for full localities and catalogue numbers). Dubious records are included at the end of the table. See text for abbreviations. Range (average ± standard deviation).

<table>
<thead>
<tr>
<th>Locality</th>
<th>Specimen</th>
<th>SVL</th>
<th>HL</th>
<th>HW</th>
<th>TL</th>
<th>Fol.</th>
<th>ED</th>
<th>TD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Valle del Cauca, via Jamundí, Sede del América</td>
<td>MHNUC He An 0133-0134</td>
<td>27.20</td>
<td>9.23</td>
<td>9.06</td>
<td>13.58</td>
<td>12.52</td>
<td>3.39</td>
<td>1.66</td>
</tr>
</tbody>
</table>

**Material and methods**

We reviewed specimens of *D. columbianus* deposited at the MHNUC and Instituto de Ciencias Naturales (ICN) collections (MHNUC-He-An R 017-18, MHNUC-He-An R 121-124). We identified the specimens following the diagnosis of *D. columbianus*: (1) head longer than it is wide; (2) toe webbing never starting at the base of the disc; (3) dorsal skin smooth with scattered small tubercles; (4) ulnar tubercles low, indistinct; (5) distal subarticular tubercle on fourth finger weakly bifid; (6) reticulations on the ventral side (Duellman and Trueb, 1973; Agudelo-Valderrama et al., 2014). Also, different descriptions of size (SVL), length of snout, shape of canthus rostralis and webbing of the toes are present in the literature (Duellman and Trueb, 1983 and Agudelo-Valderrama et al., 2014). We took the following measurements (after Duellman, 1970; Watters et al., 2016) of specimens from extra-distributional localities and from the type.
locality (Popayán), to corroborate their identification (Table 1). Measurements included: snout-vent length (SVL), head length (HL), head width (HW), tibia length (TL), interorbital distance (IOD), internarial distance (IND), eye-nostril distance (EN), foot length (FoL), eye diameter (ED), tympanum diameter (TD), thigh length (THL), snout length (SL), hand length (HAL), forearm length (FL), upper eyelid width (UEW), finger IV disk width (Fin4DW) (Table 1, Appendix 2). We compared these measurements with information from the literature (Cochran and Goin, 1970; Duellman and Trueb, 1983).

New localities.—On July 2006, we heard a chorus of males with high vocal activity in the sunset, audible from approximately 500 m at the localities of vereda Curacas (01°44'2.96"N, 77°07'33.10"W; 1050 m. a.s.l.), and Cajamarca (01°54.13°N, 77°06.58°W; 700 m. a.s.l.), both in the municipality of Mercaderes, Cauca (Fig. 1). Similarly, on December 2016, we heard active males between 18:00-21:00h in natural and artificial wetlands at vereda Quintana (02° 25’51,69”N 76°26’46,06”W – 2515 m a.s.l), municipality of Popayán, Cauca. All three localities are open pastures dedicated to livestock; in all localities, we searched actively for individuals of D. columbianus.

Distribution model.—We used all confirmed species records together with environmental data to estimate an Ecological niche model using Maxent 3.3.3e (Phillips et al., 2006), and to identify suitable habitat for D. columbianus. We used 59 of the 78 localities for the construction of the model (Appendix 1). To reduce spatial autocorrelation, we applied a spatial filtering analysis using spThin (Aiello–Lammens et al., 2015) in R software 3.3.1 (R Core Team, 2016). A minimum distance of 2 km between each record was the threshold for retaining those used in our modelling procedures. This distance was used to ensure that each cell had only one occurrence point since we used 30 arc-seconds (~1 km) spatial resolution environmental layers in the model.

To improve the ecological niche model (ENM) we used a combination of bioclimatic data and remote sensing data as environmental layers (see Buermann et al., 2008; Bisrat et al., 2012). For the bioclimatic data, we used 19 variables obtained from the WorldClim database (www.worldclim.org ver. 1.4, Hijmans et al., 2005), which are derived from monthly temperature and rainfall values (Hijmans et al., 2005). For the remote sensing data, we calculated four variables from MODIS LAI products (Leaf Area Index). The four variables represent 1 mean and 1 standard deviation (S.D.) for the high rainfall period, plus 1 mean and 1 S.D. for low rainfall period (Year: 2005). Thus, the MODIS LAI datasets (Ref: MOD15A2.A2005001.h10v08.005) (http://modis.gsfc.nasa.gov/data/dataprod/dataproducts.php?MOD_NUMBER=15) were grouped into two periods: (1) Low rainfall (January to February plus June to August) and (2) High rainfall (March to May plus September to November), as they represent the bimodal tendencies of precipitation in Colombia (Lasso, 2003). The LAI datasets describe the mean green leaf area per given land area, and represents surface photosynthesis, evapotranspiration, and habitat characteristics (Privette et al., 2002). We consider the MODIS vegetation products (e.g. LAI datasets) a proxy for humidity and a potentially good predictor of amphibian distributions (Rodriguez et al., 2005; Sillero et al., 2009). We calculated the four from the 46 MODIS LAI dataset at 1 km resolution (United States Geological Service Center for Earth Resources Observation and Science;
The accessible area (M) is the region that have been accessible by a given species via dispersal over relevant time (Barve et al., 2011; Elith et al., 2011). Here, we defined M as the Colombian ecoregions in which D. columbianus has been observed, considering that these ecoregions might act as boundaries that have repeatedly constrained the distributional potential of the species (Barve et al., 2011). We cropped the bioclimatic and LAI variables using a mask (6°34'1.2''N, 76°51'7.2''W and 1°12'21.6''N, 78°28'51.6''W) that included five ecoregions in Colombia (Olson et al., 2001): Cauca Valley dry forests, Cauca Valley montane forests, Northern Andean páramo, Northwestern Andean montane forests and Patía Valley dry forests. We used twelve descriptors to build the model (Table 2); all other descriptors did not significantly contribute to the model.

We created 25 models using Maxent 3.3.3e (Phillips et al., 2006). Maxent integrates environmental data with species locality information to give a relative measure of suitability across a study area (Phillips et al., 2006). The model was calculated applying Linear and Quadratic features, output Logistic format, bootstrap method, 25% random test, 0.5 regularization multiplier, without Do clamping, Mess or Extrapolate. A total of

Table 2. Relative contributions of environmental variables to D. columbianus Maxent model. Minimum (Min), maximum (Max), mean and standard deviation (SD) values of the environmental variables for the localities used in the model.

<table>
<thead>
<tr>
<th>Variable</th>
<th>% contribution</th>
<th>Permutation importance</th>
<th>Min</th>
<th>Max</th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature seasonality (SD x 100) (bio4)</td>
<td>26.9</td>
<td>9.2</td>
<td>214.0</td>
<td>429.0</td>
<td>30.2</td>
<td>5.2</td>
</tr>
<tr>
<td>Precipitation of warmest quarter (bio18; mm)</td>
<td>26.6</td>
<td>26.0</td>
<td>199.0</td>
<td>1056.0</td>
<td>373.0</td>
<td>186.0</td>
</tr>
<tr>
<td>LAI High rainfall (SD)</td>
<td>20.2</td>
<td>19.6</td>
<td>0.2</td>
<td>2.4</td>
<td>1.4</td>
<td>0.7</td>
</tr>
<tr>
<td>LAI Low rainfall (SD)</td>
<td>9.6</td>
<td>11.8</td>
<td>0.2</td>
<td>2.5</td>
<td>1.3</td>
<td>0.7</td>
</tr>
<tr>
<td>Precipitation of coldest quarter (bio19; mm)</td>
<td>5.5</td>
<td>12.4</td>
<td>296.0</td>
<td>1714.0</td>
<td>595.2</td>
<td>265.6</td>
</tr>
<tr>
<td>Precipitation of driest month (bio14; mm)</td>
<td>4.2</td>
<td>0.0</td>
<td>37.0</td>
<td>289.0</td>
<td>74.3</td>
<td>41.0</td>
</tr>
<tr>
<td>Precipitation of wettest month (bio13; mm)</td>
<td>3.5</td>
<td>8.7</td>
<td>133.0</td>
<td>648.0</td>
<td>237.4</td>
<td>94.1</td>
</tr>
<tr>
<td>LAI High rainfall (Mean)</td>
<td>1.0</td>
<td>5.6</td>
<td>0.6</td>
<td>5.1</td>
<td>2.4</td>
<td>1.3</td>
</tr>
<tr>
<td>LAI Low rainfall (Mean)</td>
<td>0.9</td>
<td>2.0</td>
<td>0.5</td>
<td>5.4</td>
<td>2.4</td>
<td>1.3</td>
</tr>
<tr>
<td>Mean temperature of wettest quarter (bio8; °C)</td>
<td>0.6</td>
<td>2.0</td>
<td>13.6</td>
<td>24.1</td>
<td>21.0</td>
<td>29.3</td>
</tr>
<tr>
<td>Precipitation seasonality (CV bio15)</td>
<td>0.6</td>
<td>0.6</td>
<td>24.0</td>
<td>50.0</td>
<td>35.4</td>
<td>5.8</td>
</tr>
<tr>
<td>Precipitation of driest quarter (bio17; mm)</td>
<td>0.4</td>
<td>2.0</td>
<td>154.0</td>
<td>952.0</td>
<td>269.4</td>
<td>135.1</td>
</tr>
<tr>
<td>Mean annual temperature (bio1; °C)</td>
<td>0.0</td>
<td>0.0</td>
<td>13.6</td>
<td>23.7</td>
<td>20.8</td>
<td>28.3</td>
</tr>
<tr>
<td>Mean diurnal range in temperature (bio2; °C)</td>
<td>0.0</td>
<td>0.0</td>
<td>18.6</td>
<td>31.8</td>
<td>27.6</td>
<td>31.8</td>
</tr>
<tr>
<td>Isothermality (bio3)</td>
<td>0.0</td>
<td>0.0</td>
<td>93.0</td>
<td>88.8</td>
<td>88.8</td>
<td>2.7</td>
</tr>
<tr>
<td>Maximum temperature of warmest month (bio5; °C)</td>
<td>0.0</td>
<td>0.0</td>
<td>18.6</td>
<td>31.8</td>
<td>27.6</td>
<td>31.8</td>
</tr>
<tr>
<td>Minimum temperature of coldest month (bio6; °C)</td>
<td>0.0</td>
<td>0.0</td>
<td>9.6</td>
<td>18.2</td>
<td>15.4</td>
<td>26.4</td>
</tr>
<tr>
<td>Temperature annual range (bio7; °C)</td>
<td>0.0</td>
<td>0.0</td>
<td>14.3</td>
<td>21.3</td>
<td>12.2</td>
<td>10.7</td>
</tr>
<tr>
<td>Mean temperature of driest quarter (bio9; °C)</td>
<td>0.0</td>
<td>0.0</td>
<td>14.0</td>
<td>24.3</td>
<td>21.3</td>
<td>28.4</td>
</tr>
<tr>
<td>Mean temperature of warmest quarter (bio10; °C)</td>
<td>0.0</td>
<td>0.0</td>
<td>14.1</td>
<td>24.6</td>
<td>21.6</td>
<td>28.8</td>
</tr>
<tr>
<td>Mean temperature of coldest quarter (bio11; °C)</td>
<td>0.0</td>
<td>0.0</td>
<td>13.6</td>
<td>23.7</td>
<td>20.8</td>
<td>28.3</td>
</tr>
<tr>
<td>Mean annual precipitation (bio12; mm)</td>
<td>0.0</td>
<td>0.0</td>
<td>981.0</td>
<td>5002.0</td>
<td>1763.3</td>
<td>712.7</td>
</tr>
<tr>
<td>Precipitation of wettest quarter (bio16; mm)</td>
<td>0.0</td>
<td>0.0</td>
<td>323.0</td>
<td>1714.0</td>
<td>610.2</td>
<td>260.2</td>
</tr>
</tbody>
</table>

Figure 2. Individual from Cajamarca, Mercaderes, Cauca (Photograph by F. Ayerbe-Quiñones).
10000 background points were randomly selected as background. We left all other parameters as default. We tested the accuracy of the models using the Area Under the Curve (AUC>0.75) of the Receiver Operating Characteristic (ROC) curve in Maxent (Phillips et al., 2006), which is a threshold-independent measure of a model’s ability to discriminate between absences and presences (Fielding and Bell, 1997). We retained the model with the higher AUC for both training and test data for the analysis. The selected Logistical model was transformed to boolean layers (i.e., presence-absence) with a cut-off threshold equal to the 10th percentile training presence (Redon and Luque, 2010). All geographic analyses were run in QGis (QGIS Development Team, 2016.) or R Cran (R Core Team, 2016) using the Dismo package (Hijmans et al., 2016).

Results

New localities.—Based on our fieldwork carried out in 2006 in the Patía River basin, and in vereda Quintana, Popayán municipality in 2016, we found a total of three additional localities, two of them represent new elevational records in the Department of Cauca, outside of the species’ known range. In Curacas, D. columbianus (Fig. 2) was found in artificial ponds dedicated to fish farming, whereas in Cajamarca, individuals were found in small intermittent ponds. In vereda Quintana, we searched for specimens and found two records in natural and artificial ponds dedicated for conservation and livestock activities, respectively. In the Patia river Basin we collected three specimens and deposited them in the MHNUC collection (MHNUC-He-An 533, 537, 547). In Quintana, we collected two specimens and deposited them in the ICN collection (ICN MAA 1246–1247).

Based on the review of museum specimens, we found one individual (ICN 20784) collected at vereda La Playa (2°37’2N 76°57’W), El Tambo, Department of Cauca by J. Ramirez. ICN 20784 comes from the western slopes of the Western Cordillera. This locality belongs to a different river basin (San Joaquin River) which flows into the Pacific Ocean. All these specimens have the diagnostic characters of the species, including the presence of basal webbing between digits, as observed in reviewed specimens from the type locality.
Erroneous records and localities.—Of the localities found outside the current distribution, two specimens from Guapi (MHNUC-He-An R0017-18, Department of Cauca) exhibit the characters considered diagnostic for D. columbianus (Duellman and Trueb, 1983). The measurements are also similar to those of D. columbianus from the Andes (Table 1); however, on average they had a larger TL and FoL (Table 1, Appendix 2). Since the date of collection (2 December 1989), no additional records from this region or similar habitat in adjacent departments are known (see Acosta-Galvis, 2000; Bolívar and Renjifo, 2004; Agudelo-Valderrama et al., 2014).

In contrast, the extra distributional vouchers from Quimari (n=4; MHNUC-He-An R 121-124; Department of Antioquia) are tentatively assigned to D. phlebodes because they exhibit a visible tympanum, the webbing of the fingers does not begin at the disk and the presence of mid-length webbing between the finger I and II and III – IV. The colour in preservation is dark brown on both ventral and dorsal surfaces (vinaceous drab with a coarse network of dark purplish reticulations according Stejneger, 1906); the skin is aerolate on the ventral side and smooth on the dorsal surface. However, the head is longer than it is broad.

Distribution model.—The temperature seasonality (SD x 100) (Bio4) (26.9%), precipitation in the warmest quarter (Bio18) (26.6%) and LAI during high rainfall (20.2%) showed the highest contribution percentages (Table 2). D. columbianus occurs in regions with temperature seasonality (SD x 100) (Bio4) between 21.4–42.0 °C, precipitation in the warmest quarter (Bio18) between 199–1056 mm and LAI during high rainfall (SD) between 0.23–2.37 (Table 2).

Both, AUC training data (0.83) and AUC testing data (0.81) of the selected Maxent model, showed values better than random (AUC>0.5). The threshold equal to the 10th percentile training presence applied as a cut-off for the model was 0.235. The pixels with the highest probabilities are concentrated around the Cauca and Patía rivers (Fig. 3). The Maxent model for D. columbianus predicted the potential distribution of the species in the lowlands located between the Central and Western Cordilleras of Colombia along the Cauca River (Fig. 4). In addition to the previous distribution records, our model suggests that there are others suitable potential localities in Andean ecoregions, like the inter-Andean valleys of Nariño and Antioquia. According to the model, dry and montane environments located in the slopes of the western Colombia are unsuitable for the species and provide a natural barrier for species dispersion to Eastern Cordillera (Fig. 4).

Discussion

Our records add new localities of D. columbianus in two different river basins (Patía and San Joaquín rivers), confirm the occurrence of the species in the inter-Andean valley of the Patía River in the department of Cauca (Kattan, 1984; Guerrero-Vargas et al., 2007), and indicate, for the first time, the occurrence of D. columbianus in the San Joaquin River. From the Patía River basin, only one specimen (MHNUC-He-An 452), collected on the 3rd of August 2005, was previously known (Guerrero-Vargas et al., 2007). Records from Mercaderes (Cauca) also represent the lowest elevation (700 m) ever recorded for the species, and extend the distribution of the species 40 km to the south of previously known records at Finca Hawai (02°05´ N, 77°0.28´ W, 900 m. a.s.l.), municipality of Patía, Cauca (Guerrero-Vargas et al., 2007). The locality of vereda Quintana (ICN MAA 1246–1247) represents the highest record (2500 m) in the Andes region of Colombia, and extends the elevational distribution of the species with 160 m compared to previous altitudinal records (Duellman and Trueb, 1983; Acosta-Galvis, 2000; Bolívar and Renjifo, 2004; Agudelo-Valderrama et al., 2014; Frost, 2016). The locality from La Playa (ICN 20784) represents the westernmost record for the species and extends its distribution to the eastern slopes of Western Cordillera.

Records from Guapi, in the Biogeographic Chocó region are controversial because seemingly, the localities of these records seem to be mistakenly confused in the field notes of the collector or during inclusion of the two available specimens into the MHNUC catalogues. We believe this because other additional species known only from the Andean region (i.e. Pristimantis w-nigrum) deposited at the MHNUC (MHNUC He An 014-016) also appear as collected at the lowlands of Guapi (in the biogeographic Chocó region) in the MHNUC catalogues. The alternative, a scenario in which a similar-looking species of the D. columbianus species group is distributed in the Biogeographic Chocó region of the Department of Cauca is unlikely. Although there is one specie of the D. columbianus complex distributed in the Chocó of Ecuador (i.e. D. carnifex), the presence of small tubercles on the dorsum and absence of spots on the upper lip of the specimens MHNUC He An 017-018 (see Duellman, 1969) indicate that both are not D. carnifex. Therefore, we suggest that the records from
Guapi are based on erroneous information. Furthermore, we found no valid records of *D. columbia*us outside the Andean region of Colombia. Available records come from the departments of Caldas, Cauca, Quindío, Risaralda and Valle del Cauca (Fig. 1). Similarly, the results of the distribution model show a strong association of the species to Andean ecoregions and exclude its presence from the Chocó region. The model suggests that temperature seasonality, the precipitation of the warmest quarter and the LAI measured during high rainfall periods are important climatic variables for the species and confirms that *D. columbia*us is typically associated with open areas and grassy marshes (Bolívar and Renjifo, 2004), where humidity and vegetation depends directly of the amounts of rainfall.

The potential distribution of the species extends from Nariño to Antioquia following the Cauca River basin. We believe that the southern populations of the species in Nariño are restricted by the Patía, Pasto and Guáitara Rivers in the Nudo de los Pastos, because both are natural barriers to the dispersion of other animals (Lynch, 1981; Ramírez-Chaves and Noguera-Urban, 2010; Noguera-Urban, 2016). Finally, even though the distribution model shows that the presence of *D. columbia*us in Antioquia is likely, the northern boundary of the species distribution is unclear due to the absence of records. Future expeditions will be necessary to verify the presence of the species in these regions.

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**References**


Appendix 1. Localities (plotted in Figure 1) of *Dendropsophus columbianus*. The symbol (*) indicate training data used in building of the ecological niche model.

**COLOMBIA:** Department of Cauca: 1. La Cabuyera* (2°31′00″N, 76°34′26″W; Guerrero-Vargas et al., 2007); 2. Cajamarca (1°54′13″W, 77°06′58″N; 700 m); 3. Caloto (2°50′49″N, 76°24′25″W; Agudelo-Valderrama et al., 2014); 4. Curacas, Mercaderes (01°44′03″N, 77°07′58″W; 700 m); 5. Guapi (4°32′45″N, 75°39′44″W; Guerrero-Vargas et al., 2007); 6. Patía, Finca Hawai* (2°05′N, 77°02′8″W; 900 m; Guerrero-Vargas et al., 2007); 7. Popayán* (02°27′N, 76°36′28″W; 1750-1850 m; Type locality); 8. Popayán* (2°28′28″N, 76°35′14″W; Guerrero-Vargas et al., 2007); 9. Popayán* (2°32′30″N, 76°24′06″W; Guerrero-Vargas et al., 2007); 10. Popayán (2°32′54″N, 76°24′37″W; Guerrero-Vargas et al., 2007); 11. Popayán (2°36′41″N, 76°36′01″W; Guerrero-Vargas et al., 2007); 12. Popayán (2°36′11″N, 76°35′37″W; Guerrero-Vargas et al., 2007); 13. Santander de Quilichao (3°00′08″N, 76°28′40″W; Agudelo-Valderrama et al., 2014); 14. Totoró* (02°30′N, 76°24′W, 1797 m; Guerrero-Vargas et al., 2007); 15. Timbio* (2°23′28″N, 76°39′18″W; Agudelo-Valderrama et al., 2014); 16. El Tambo, road to Munchique* (02°27′N, 76°49′W; 2350 m; Duellman and Trueb, 1983); 17. El Tambo (2°45′05″N, 76°56′47″W; Guerrero-Vargas et al., 2007); 18. El Tambo (2°44′52″N, 76°56′35″W; Guerrero-Vargas et al., 2007).

Department of Valle del Cauca: 20. Argelia (4°38′55″N, 76°07′30″W; Agudelo-Valderrama et al., 2014); 21. Agua Salada, Yotoco* (3°54′12″N, 76°20′48″W; Agudelo-Valderrama et al., 2014); 22. Buga (3°49′10″N, 76°18′21″W; Agudelo-Valderrama et al., 2014); 23. Bocas de Tuluá* (4°09′31″N, 76°14′28″W; Agudelo-Valderrama et al., 2014); 24. Cali* (03°27′N, 76°32′W; 1000 m; Agudelo-Valderrama et al., 2014); 25. Cartago, La Castilla (4°47′30″N, 75°55′23″W; Agudelo-Valderrama et al., 2014); 26. Chicoral* (3°38′24″N, 76°35′19″W; Agudelo-Valderrama et al., 2014); 27. Candelaria (03°25′N, 76°20′W; 975 m; Duellman and Trueb, 1983); 28. El Cairo, Diamantina 1* (4°47′15″N, 76°12′14″W; Agudelo-Valderrama et al., 2014); 29. Estación Piscícola de Buga (3°33′57″N, 75°38′24″W; Agudelo-Valderrama et al., 2014); 30. Finca El Coronel (4°13′56″N, 76°11′08″W; Agudelo-Valderrama et al., 2014); 31. Finca El Grande (4°11′44″N, 76°05′25″W; Agudelo-Valderrama et al., 2014); 32. Jamundi* (3°13′18″N, 76°35′59″W; Agudelo-Valderrama et al., 2014); 33. La Nubia* (3°55′13″N, 76°20′21″W; Agudelo-Valderrama et al., 2014); 34. Lago Calima (3°53′40″N, 76°29′41″W; 1350 m; Duellman and Trueb, 1983); 35. Lago Cantarana* (4°11′44″N, 76°05′25″W; Agudelo-Valderrama et al., 2014); 36. Lagos El Amparo, El Cairo* (4°47′15″N, 76°12′14″W; Agudelo-Valderrama et al., 2014); 37. Lagos km 18, Vía Rio Frío (04°06′41″N, 76°18′23″W; Agudelo-Valderrama et al., 2014); 38. Laguna Hogar CAM, Cartago (4°47′30″N, 75°55′23″W; Agudelo-Valderrama et al., 2014); 39. Madrevieja Badeal* (4°47′29″N, 75°55′22″W; Agudelo-Valderrama et al., 2014); 40. Madrevieja Chiquique (3°49′51″N, 76°23′15″W; Agudelo-Valderrama et al., 2014); 41. Madrevieja Gota de Leche* (3°47′17″N, 76°23′33″W; Agudelo-Valderrama et al., 2014); 42. Madrevieja Guare (4°20′49″N, 76°09′43″W; Agudelo-Valderrama et al., 2014); 43. Madrevieja Higuercntico* (3°34′41″N, 76°27′46″W; Agudelo-Valderrama et al., 2014); 44. Madrevieja La Isabel* (3°53′18″N, 76°19′26″W; Agudelo-Valderrama et al., 2014); 45. Madrevieja La Marina, Laguna de Sonso* (3°52′46″N, 76°20′46″W; Agudelo-Valderrama et al., 2014); 46. Madrevieja Madrigal, Rio Frío (4°10′50″N, 76°15′25″W; Agudelo-Valderrama et al., 2014); 47. Madrevieja Remolino* (4°28′25″N, 76°05′14″W; Agudelo-Valderrama et al., 2014); 48. Madrevieja Ricaurte* (4°17′15″N, 76°12′24″W; Agudelo-Valderrama et al., 2014); 49. Madrevieja Tiber* (4°02′17″N, 76°18′01″W; Agudelo-Valderrama et al., 2014); 50. Media Canoa; Yotoco (3°53′12″N, 76°19′48″W; Agudelo-Valderrama et al., 2014); 51. Microestación Univalle, Melendez (3°22′40″N, 76°32′11″W; Agudelo-Valderrama et al., 2014); 52. Sanjón Burriga* (3°56′13″N, 76°21′21″W; Agudelo-Valderrama et al., 2014); 53. Tuluá (4°09′N, 75°54′03″W; Agudelo-Valderrama et al., 2014); 54. Vereda El Eglo, Finca El Topacio* (4°39′58″N, 75°43′22″W; MPUJ-ANFB 7129); 55. Vereda El Nogal, Finca El Topacio* (3°53′12″N, 76°19′48″W; Agudelo-Valderrama et al., 2014); 56. Vereda El Nogal, Finca El Topacio* (4°39′58″N, 75°43′22″W; MPUJ-ANFB 7129); 57. Vereda El Nogal- Finca El Topacio* (4°40′24″N, 75°43′63″W*; MPUJ-ANFB 7637, 7648, 7649, 7650, 7651); 58. Yotoco (3°53′12″N, 76°19′48″W; Agudelo-Valderrama et al., 2014); 59. Armenia (4°32′45″N, 75°39′44″W; Agudelo-Valderrama et al., 2014); 60. Circasia (3°37′57″N, 75°38′24″W; Agudelo-Valderrama et al., 2014); 61. Quimbaya-
Appendix 2. Additional specimens examined.

*Dendropsophus columbianus* (n = 31): **Cauca**, El Tambo, Piagua, Maesta Vida (02°26′N, 76°45′W; 1715 m [MHNUC-He-An 001033-1037 ♀♀]); **Cauca**, Mercaderes, Cajamarca (1°54′13″N, 77°06′58″W; 700 m [MHNUC-He-An 0537 ♂♀]; **Cauca**, Mercaderes, Hacienda Curacas (01°44′2.96″N, 77°7′33.10″W; 1050 m [MHNUC-He-An 0533 ♂♀, MHNUC-He-An 0547 ♂♀]); **Cauca**, Patia, Finca Hawai (02°05′54″N, 77°00′25″W; 800 m [MHNUC-He-An 0452 ♂♀]); **Cauca**, Popayán, Hacienda La Paz, via la Variante (02°28′28″N 76°35′14″W; 1850 m [MHNUC-He-An 085-89 ♂♀]); **Cauca**, Popayán, La Cabuyera, El Cofre (02°31′0.4″N, 76°34′26″W; 1700 m [MHNUC-He-An 0145-147 ♂♂, 0151-152 ♂♀]); **Cauca**, Sotará, Paispamba, Hatofrio (02°16′N, 76°35′W; 1700 m, 2300 m [MHNUC-He-An 0648-652 ♂♀]); **Cauca**, Totoró, Resguardo Indígena Novirao (02°31′N, 76°29′W; 1797 m [MHNUC-He-An 0408-0412 ♂]); **Valle del Cauca**, via a Jamundí, Sede del América (03°8′57″N, 76°31′16″W; 1050 m [MHNUC-He-An 0133, ♂ MHNUC-He-An 0134, ♀]).

Dubious records and localities assigned to *D. columbianus* in literature (n = 6).

Colombia: **Córdoba**, Quimari (08°07′N, 76°23′W; 400-700 m [MHNUC-He-An 0121-124 ♀♀]); **Cauca**, Guapi (02°35′0.4″N, 77°54′16.5″W; 100 m [MHNUC-He-An R017-18 ♀♀]).