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# Acoustic repertory of the "*Colostethus*" *ruthveni* group (Anura: Dendrobatidae) and comments on the distribution in the Sierra Nevada de Santa Marta, Colombia

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**Abstract.** The "*Colostethus*" *ruthveni* group represents an endemic dendrobatid lineage in the Sierra Nevada de Santa Marta (SNSM), an isolated massif in northeastern Colombia. This group has a complex taxonomic history and comprises the nominal species, from the northern and northwestern sector of the SNSM and an undescribed morph provisionally named as "*Colostethus*" sp. *ruthveni*-like, from the southeastern sector of this mountain massif. Herein, we describe the advertisement calls of members of the "*C.*" *ruthveni* group from several basins in the northern, northwestern, and southeastern sectors of the SNSM, and their geographic variation. In addition, we describe the courtship calls of the northwestern populations and provide comments on the distribution of the members of the group. The advertisement call of the "*C.*" *ruthveni* group consists of a trill with a long series of notes. All advertisement call traits show statistical differences among the assessed basins. The principal component analysis revealed overlap in call traits of individuals from the northwestern sector of the SNSM ("*C.*" *ruthveni* sensu stricto), while the populations of the southeastern sector ("*C.*" sp. *ruthveni*-like) and northern sector ("*C.*" cf. *ruthveni*) varied from these calls with respect to the dominant frequency and rate of notes per second, respectively. Acoustic divergence of advertisement calls of "*C.*" *ruthveni* sensu stricto and "*C.*" sp *ruthveni*-like is congruent with morphological and molecular evidence. Courtship call of "*C.*" *ruthveni* sensu stricto is a short partially fused pulsed squeak, followed by the usual advertisement call. This courtship call differs drastically in structure from the advertisement call, showing once again the complexity of the acoustic repertory of dendrobatoid frogs.

Key words. Acoustic divergence, advertisement call, Colombian Caribbean, courtship call, geographic variation.

## Introduction

The Sierra Nevada de Santa Marta (SNSM) is an isolated mountain massif in northeastern Colombia, in the departments of Magdalena, Cesar and La Guajira. Edaphic and climatic conditions of this mountain system promote speciation processes, resulting in an eco-geographic area with high endemicity (Carbonó & Lozano-Contreras 1997, Lynch et al. 1997). According to Armesto & Señaris (2017), the SNSM has the highest proportion of endemic anurans within the northern Andes. One of these endemic lineages is the "*Colostethus*" *ruthveni* group, composed of the homonym species (Kaplan, 1997) and at least one undescribed morph (Lynch et al. 1997, Grant et al. 2017). The complex history of this group started in the early 20th century, with the description of the back-riding tadpoles (Ruthven & Gaige 1915) and some aspects of the natural history (Ruthven 1922) of "*C.*" *ruthveni* in the northern and northwestern sectors of the SNSM, under the identity of *Hyloxalus subpunctatus* (Cope, 1899).

The formal description of "*Colostethus*" *ruthveni* by Kaplan (1997) was based on specimens mainly collected in the northwestern sector of the SNSM (type locality: quebrada Viernes Santo, Santa Marta, Magdalena department) in the early 20th century and housed in the Museum of Zoology of the Michigan University (UMMZ). Later, some contributions to the distribution (González-Maya et al. 2011, Granda-Rodríguez et al. 2014) and feeding ecology (Blanco-Torres et al. 2014) of "*C.*" *ruthveni* were published. Rueda-Almonacid et al. (2008) provided a brief


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morphological description of an undescribed dendrobatoid species, temporarily named "*Allobates* sp." from a locality in the southeastern foothills of the SNSM (Los Besotes Eco-park, Valledupar, Cesar department). In contrast, Anganoy-Criollo (2012, therein see Appendix A) and Granda-Rodríguez et al. (2014) referred to specimens from another locality in the southeastern sector of SNSM (Nabusímake, Valledupar, 22.7 km in straight line of Los Besotes) as "*C.*" *ruthveni*. This situation generated uncertainty about the taxonomic status of the populations of the southern region of the SNSM.

In a recent phylogenetic reconstruction of the Dendrobatoidea, Grant et al. (2017), proposed that the "*Colostethus*" *ruthveni* group is not related with the "colostethines" (or any other group of dendrobatoid frogs with cryptic coloration), but constitutes an undescribed genus closely related to toothless dendrobatines (tribe Dendrobatini sensu Grant et al. 2017). The authors agreed with Rueda-Almonacid et al. (2008) in that the population from Los Besotes corresponds to an undescribed species, provisionally naming it "*Colostethus*" sp. *ruthveni*-like.

The importance of acoustic signals in intraspecific social functions of anurans has been highlighted as being potentially useful for species recognition and taxonomic decision making (Padial et al. 2009, Forti et al. 2017, Köhler et al. 2017). In allopatric speciation scenarios, call differences are tricky to interpret as they do not necessarily indicate specific distinctness, because separated populations of the same species can adapt to different environmental conditions by modifying their vocalizations (Bernal et al. 2005, Köhler et al. 2017). Nevertheless, we here start from the initial assumption that interspecific variation in bioacoustic characters exceeds intraspecific variation (cf. Köhler et al. 2017). To elucidate the taxonomic status and the delimitation of species within the "*C.*" *ruthveni* group, this research was conducted in five hydrographic basins of the SNSM with the objectives (1) to describe the advertisement call and the geographic variation of call traits of

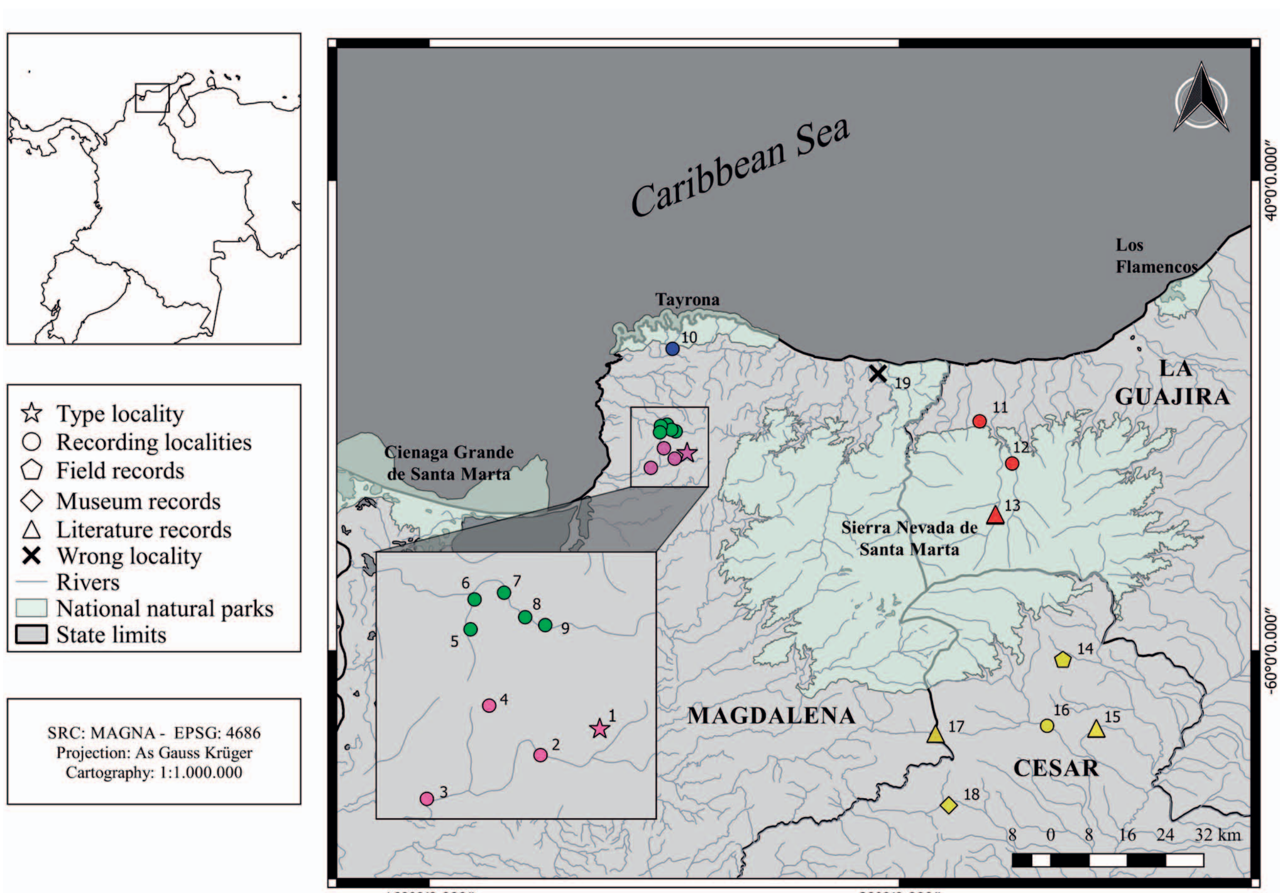


Figure 1. Referred localities with presence of members of "*Colostethus*" *ruthveni* group in the SNSM (departments of Cesar, La Guajira and Magdalena, Colombia). Toribio basin (violet): 1. Viernes Santo creek (type locality), 2. La Tagua Village, 3. Hacienda El Aserrío, 4. Hacienda El Recuerdo; Gaira basin (green): 5. Arimaca, 6. El Berro creek, 7. Pozo Azul, 8. Hacienda La Victoria, 9. El Campano Village; Los Rodríguez basin (blue): 10. Las Tinajas Village; Ancho basin (red):11. Tugueca Village, 12. Wimangaga Reserve, 13. San Miguel Village; Cesar basin (yellowish): 14. Atanquez Village, 15. Los Besotes Eco-park, 16. Donachuí Village, 17. Nabusímake Village, 18. Pueblo Bello Village, 19. Don Diego Village.

Table 1. Localities where calls of the members of the "*Colostethus*" *ruthveni* group were recorded. *Information on the courtship call in parenthesis.

| Locality | Geographic coordinates (Datum WGS84) | Elevation (m a.s.l.) | N males | N calls | Hour | Temperature (°C) |
|---|---|---|---|---|---|---|
| Gaira river basin | | | | | | |
| El Campano Village | 11°6'41.41"N, 74°5'36.24"W | 1450 | 1 | 2 | 11:15–11:20 | 28.3 |
| Hacienda La Victoria | 11°7'44.10"N, 74°5'32.40"W | 900 | 3 | 8 | 08:40–09:00 | 24.7 |
| Pozo Azul | 11°7'58.72"N, 74°6'07.58"W | 836 | 2 | 12 | 09:30–09:50 | 25.1 |
| Arimaca* | 11°7'33.56"N, 74°7'08.93"W | 723 | 3 (1) | 12 (4) | 15:15–15:30 | 24.6 |
| El Berro creek | 11°8'18.33"N, 74°7'00.88"W | 620 | 2 | 12 | 14:45–15:00 | 26.5 |
| Toribio river basin | | | | | | |
| La Tagua Village | 11°4'55.00"N, 74°2'22.70"W | 1500 | 3 | 11 | 08:30–08:40 | 23.9 |
| Hacienda El Aserrío | 11°4'56.80"N, 74°6'41.90"W | 1400 | 4 | 10 | 15:40–15:50 | 26.5 |
| Hacienda El Recuerdo | 11°5'14.00"N, 74°2'53.00"W | 1200 | 1 | 5 | 09:20–09:30 | 25.6 |
| Los Rodríguez creek basin | | | | | | |
| Las Tinajas Village | 11°17'03,80"N, 74°4'00,20"W | 735 | 5 | 11 | 10:15–10:30 | 28.2 |
| Ancho river basin | | | | | | |
| Wimangaga Reserve | 11°8'18.42"N, 73°32'45.94"W | 700 | 2 | 11 | 09:00–09:15 | 25.6 |
| Tugueca Village | 11°8'49.11"N, 73°30'32.68"W | 450 | 1 | 12 | 10:20–10:30 | 29.3 |
| Cesar river Basin | | | | | | |
| Donachuí Village | 10°42'47.60"N, 73°27'20.64"W | 1436 | 3 | 6 | 16:40–16:50 | 27.2 |

the members of the "*C.*" *ruthveni* group, (2) to evaluate the potential acoustic divergence between "*C.*" *ruthveni* from the northern and northwestern sector of the SNSM and "*C.*" sp. *ruthveni*-like, (3) to provide a description of the courtship call from populations of the northwestern sector of SNSM, and (4) to add information on the distribution of the group members.

## Materials and methods

### Study area

Advertisement calls (AC) of specimens of the "*Colostethus*" *ruthveni* group were recorded at different localities in the northern, northwestern, and southeastern sectors of the SNSM (Table 1, Fig. 1). In the northwestern sector (Santa Marta district, Magdalena department), recordings were conducted at five localities in the middle Gaira river basin, at three localities in the middle Toribio river basin, and at one locality in the upper Los Rodríguez creek basin. In the northern sector (Dibulla municipality, La Guajira department), calls were recorded at two localities from the lower and middle Ancho river basin. In the southeastern sector (Valledupar municipality, Cesar department), recordings were conducted at one locality in the upper Cesar river basin. The courtship call (CC) was recorded in Arimaca, in the middle Gaira river basin in the northwestern sector (Table 1, Fig. 1). The midlands of the northwestern sector and the lowlands of the northern sector of the SNSM have humid forest formations, while the southwestern sector shows vegetation related to tropical dry forest formations (Hernández-Camacho et al. 1992).

### Call collection and analyses

Calls of 30 males with a duration of in total 40 min. were recorded with a Tascam DR05 recorder during seven field trips between December 2014 and April 2017; recordings were made at 08:00–12:00 h and 15:00–17:00 h, at an approximate distance of 50 cm from the calling male (Table 1). Air temperature was measured with a digital thermo-hygrometer Extech RH210. Voucher specimens were not collected and each male at each site was only recorded once to avoid pseudoreplication. To complement the taxonomic framework of the calls, available specimens of the "*Colostethus*" *ruthveni* group in the amphibian collection of the Centro de Colecciones Biológicas de la Universidad del Magdalena (CBUMAG:ANF) were revised, including specimens from the same (or nearby) localities of the recorded calls.

All calls were analyzed with Praat (v. 6.0.13) for windows (Boersma, P. & D. Weenink 2007: Praat: Doing phonetics by computer; available from http://www.fon.hum.uva.nl/praat/; accessed April 2015) at a sampling frequency of 44.1 kHz and 16 bits resolution. We consider continuous vocalizations performed by males to attract females as AC, and particular vocalizations emitted by males in the presence of females as CC (Wells 2007, Köhler et al. 2017). Each call was extracted from the original recording as an individual file. For each call, the following traits were measured: call duration (in seconds = s), number of notes per call, rate of notes per second (notes/s), note duration (s), internote interval (s), dominant frequency (Hz), and visible harmonics. Means, standard deviation (SD), and coefficient of variation (CV) were calculated for each call trait.

Call traits with CV ≤ 0.05 were considered as static traits (cf. Gerhardt 1991). We follow the terminology proposed and revised by Lötters et al. (2003) for advertisement call types and Köhler et al. (2017) for call traits.

A Kruskal-Wallis test (H) was performed to evaluate the potential geographic variation of the AC of the members of the "*C.*" *ruthveni* group, in order to refuse the null hypothesis that no differences in call traits (note duration, internote interval, rate of notes per second, and dominant frequency) exist between different basins. As post hoc analysis, a pairwise Wilcoxon test was conducted. Both tests were performed with the 'basic' package for the Cran R platform, analyzing each note individually. To reduce the variation of call traits and visualize potential cluster in terms of similarity, a principal component analyses (PCA) of the mean values of call traits was performed for each male. This analysis was conducted with the 'Factoextra' package for Cran R (Kassambara, A. & F. Mundt 2017: Factoextra: extract and visualize the results of multivariate data analyses. R package version 1.0.5; available from https://CRAN.R-project.org/package=factoextra; accessed June 2017). Spectrograms and oscillograms were obtained with the 'Seewave' package for Cran R (Sueur et al. 2008).

## Results

### Advertisement call

In the first instance, no obvious qualitative differences were detected in the AC of the populations assigned to the "*Colostethus*" *ruthveni* group (Fig. 2). Nevertheless, significant variation was detected in certain quantitative call traits among individuals in the basins assessed (Table 2). The Kruskal-Wallis test showed significant differences in note duration between the different populations (H = 1313, df [degrees of freedom] = 4, p < 0.001, Fig. 3a). According to the grouping by significance of the pairwise Wilcoxon test, all basins showed differences among themselves (all

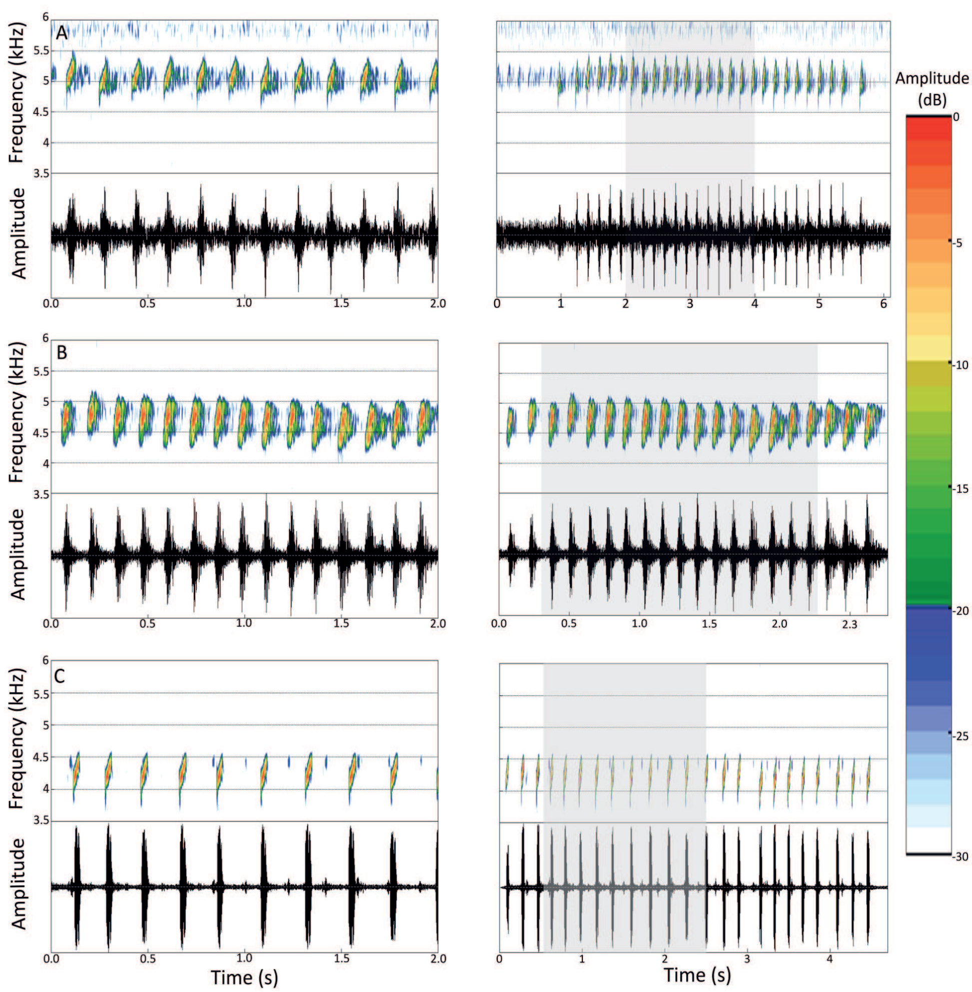


Figure 2. Spectrograms and oscillograms of the advertisement calls of "*Colostethus*" *ruthveni* sensu stricto (A, El Berro creek, Minca Village, Gaira basin, Santa Marta, Magdalena), "*Colostethus*" cf. *ruthveni* (B, Tugueca village, Río Ancho basin, Dibulla, La Guajira), and "*Colostethus*" sp. *ruthveni*-like (C, Donachuí village, Cesar basin, Valledupar, Cesar). Two seconds fragments (left) and entire calls (right) for each group. Grayish area shows the two seconds fragment within the call.

Table 2. Variation of the advertisement call traits of the members of the "*Colostethus*" *ruthveni* group by basins.

| Basin | N | Mean | SD | Minimums | Maximums | CV | Grouping by Wilcoxon pairwise test |
|---|---|---|---|---|---|---|---|
| Note duration (s) | | | | | | | |
| Ancho | 478 | 0.029 | 0.005 | 0.017 | 0.083 | 0.183 | a |
| Gaira | 1203 | 0.067 | 0.024 | 0.02 | 0.17 | 0.35 | b |
| Cesar | 119 | 0.025 | 0.01 | 0.009 | 0.046 | 0.397 | c |
| Los Rodríguez | 312 | 0.059 | 0.011 | 0.028 | 0.098 | 0.181 | d |
| Toribio | 482 | 0.054 | 0.014 | 0.02 | 0.097 | 0.255 | e |
| Kruskal-Wallis test | H = 1313, df = 4, p < 0.001 | | | | | | |
| Internote interval (s) | | | | | | | |
| Ancho | 455 | 0.090 | 0.016 | 0.056 | 0.189 | 0.179 | a |
| Gaira | 1159 | 0.122 | 0.039 | 0.053 | 0.445 | 0.322 | b |
| Cesar | 113 | 0.153 | 0.043 | 0.074 | 0.419 | 0.278 | c |
| Los Rodríguez | 302 | 0.144 | 0.027 | 0.045 | 0.247 | 0.188 | c |
| Toribio | 457 | 0.203 | 0.081 | 0.064 | 0.625 | 0.399 | d |
| Kruskal-Wallis test | H = 1265.1, df = 4, p < 0.001 | | | | | | |
| Rate of notes per second (notes/s) | | | | | | | |
| Ancho | 23 | 8.673 | 0.760 | 7.607 | 9.713 | 0.088 | a |
| Gaira | 45 | 6.003 | 1.629 | 4.172 | 12.953 | 0.271 | b |
| Cesar | 6 | 5.603 | 1.069 | 3.701 | 6.564 | 0.191 | bc |
| Los Rodríguez | 11 | 4.998 | 0.101 | 4.847 | 5.142 | 0.02 | d |
| Toribio | 26 | 4.462 | 1.487 | 2.643 | 9.631 | 0.333 | c |
| Kruskal-Wallis test | H = 64.263, df = 4, p < 0.001 | | | | | | |
| Dominant frequency (Hz) | | | | | | | |
| Ancho | 478 | 4909.584 | 279.119 | 4180 | 5307 | 0.057 | a |
| Gaira | 1203 | 5030.381 | 195.643 | 4600 | 5539 | 0.039 | b |
| Cesar | 119 | 4301.160 | 90.273 | 3979 | 4487 | 0.021 | c |
| Los Rodríguez | 312 | 5742.763 | 95.075 | 5402 | 5944 | 0.017 | d |
| Toribio | 482 | 4732.770 | 279.575 | 4157 | 5238 | 0.059 | e |
| Kruskal-Wallis test | H = 1302.2, df = 4, p < 0.001 | | | | | | |

pairwise tests with p < 0.001). Note duration was a dynamic call trait, showing a considerable variation even among individuals within each basin (CV = 0.181–0.397). The result for internote intervals was similarly variable between most basins (H = 1265.1, df = 4, p < 0.001, Fig. 3b), with only one pair of basins that did not differ from each other (Cesar vs. Los Rodríguez, p = 0.08). This call trait also exhibited considerable variation among individuals within each basin (CV =0.179–0.399).

The differences in the rate of notes per second were remarkable between the basins (H = 64.263, df = 4, p < 0.001, Fig. 3c), but presented a slightly smaller variation than the call traits mentioned above within each basin (CV = 0.088–0.333). There were no differences between Gaira vs. Cesar (p = 0.804) and between Cesar vs. Toribio (p = 0.057). Finally, the dominant frequency also differed between all basins (H = 1302.2, df = 4, p < 0.001, Fig. 3d), although this call trait showed the smallest variation (almost static) within each basin (CV < 0.06 in all basins).

Variation of note duration, internote interval, rate of notes per second, and dominant frequency of the AC of the members of the "*Colostethus*" *ruthveni* group was well summarized by three dimensions of the PCA (Table 3, Fig. 4). Internote interval and rate of notes per second were mainly explained by dimension 1, while note duration and dominant frequency were mainly explained by dimensions 2 and 3. The first two dimensions explained 84.84% of the variance in the PCA (Table 3). Results of the PCA reflect that call traits of individuals from Gaira and Los Rodríguez basins are heavily overlapping, whereas individuals from Gaira and Toribio basins showed only a slight overlap, and

Table 3. Results of the principal components analysis, summarizing the variation of the advertisement calls of the members of the "*Colostethus*" *ruthveni* group.

| Call trait | Dim.1 | Dim.2 | Dim.3 |
|---|---|---|---|
| Note duration (s) | -0.175 | 0.874 | -0.445 |
| Internote interval (s) | -0.947 | -0.143 | 0.194 |
| Rate of notes per second (notes/s) | 0.449 | 0.737 | 0.503 |
| Dominant frequency (Hz) | 0.903 | -0.347 | -0.133 |
| Eigenvalues | 1.945 | 1.448 | 0.507 |
| Explained variance (%) | 48.633 | 36.206 | 12.676 |

those from Cesar and Ancho basins were positioned separately, varying in their dominant frequency and rate of notes per second, respectively (Fig. 4). These results support the divergence of populations from the northwestern sector of the SNSM (hereinafter named "*C.*" *ruthveni* sensu stricto, Fig. 5a) and the southwestern sector ("*C.*" sp. *ruthveni*-like, Fig. 5b). Surprisingly, the PCA revealed particular acoustic features of males from the northern sector (hereinafter named "*C.*" cf. *ruthveni*, Fig. 5c).

The AC of members of the "*Colostethus*" *ruthveni* group consists of a long series of trills with pulsating notes and modulated amplitude (Table 4, Fig. 2). In "*C.*" *ruthveni* sensu stricto the mean duration of the AC was 4.868 s (SD = 2.358 s), with a mean of 25 notes per call (SD = 11 notes), a mean note duration of 0.063 s (SD = 0.021 s), a mean rate of 5.380 notes per second (SD = 1.622 notes/s), and internote intervals of 0.145 s (SD = 0.061 s). Call frequency was in the spectral band between 3,000–16,000 Hz. Notes

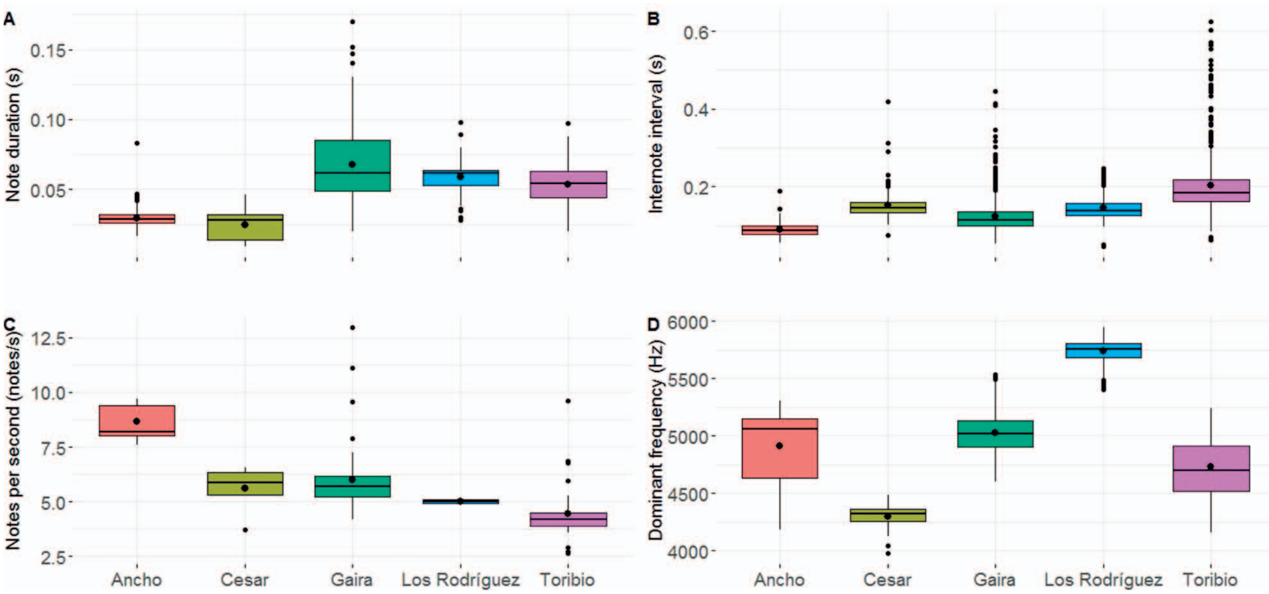


Figure 3. Geographic variation of note duration (A), internote interval (B), rate of notes per second (C), and dominant frequency (D). Colors and names of X axis correspond to information in Table 1 and Figure 1.

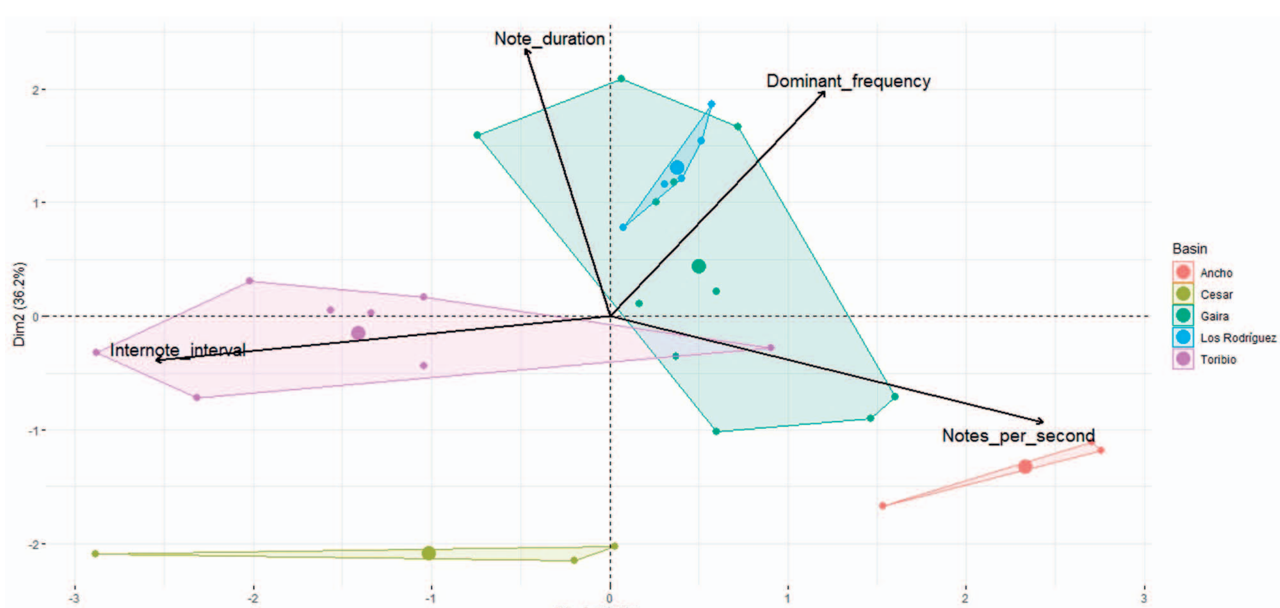


Figure 4. Variation of the advertisement call traits explained by two principal components. Colors and names correspond to information in Table 1 and Figure 1.

Table 4. General data of the advertisement calls of the members of the "*Colostethus*" *ruthveni* group.

| Call trait | N | Mean | SD | Minimums | Maximums | CV |
|---|---|---|---|---|---|---|
| "*Colostethus*" *ruthveni* sensu stricto | | | | | | |
| Call duration (s) | 82 | 4.868 | 2.358 | 1.036 | 12.464 | 0.484 |
| Notes per call | 82 | 25 | 11 | 5 | 52 | 0.452 |
| Rate of notes per second (notes/s) | 82 | 5.380 | 1.622 | 2.643 | 12.953 | 0.302 |
| Note duration (s) | 1997 | 0.063 | 0.021 | 0.020 | 0.170 | 0.332 |
| Internote interval (s) | 1918 | 0.145 | 0.061 | 0.045 | 0.625 | 0.421 |
| Dominant frequency (Hz) | 1997 | 5069.847 | 377.427 | 4157 | 5944 | 0.074 |
| Harmonic 1 | 1857 | 7648.673 | 581.536 | 5448 | 9947 | 0.076 |
| Harmonic 2 | 850 | 9594.842 | 611.093 | 4988 | 12949 | 0.064 |
| Harmonic 3 | 504 | 12680.165 | 456.792 | 11045 | 15142 | 0.036 |
| Harmonic 4 | 493 | 14970.233 | 354.457 | 13745 | 17139 | 0.024 |
| "*Colostethus*" sp. *ruthveni*-like | | | | | | |
| Call duration (s) | 6 | 3.363 | 1.578 | 1.351 | 4.773 | 0.469 |
| Notes per call | 10 | 20 | 11 | 5 | 30 | 0.546 |
| Rate of notes per second (notes/s) | 10 | 5.603 | 1.069 | 3.701 | 6.564 | 0.191 |
| Note duration (s) | 119 | 0.025 | 0.010 | 0.009 | 0.046 | 0.397 |
| Internote interval (s) | 113 | 0.153 | 0.043 | 0.074 | 0.419 | 0.278 |
| Dominant frequency (Hz) | 119 | 4301.160 | 90.273 | 3979 | 4487 | 0.021 |
| Harmonic 1 | 119 | 8196.504 | 104.165 | 7925 | 8404 | 0.013 |
| Harmonic 2 | 119 | 12091.546 | 109.780 | 11794 | 12314 | 0.009 |
| Harmonic 3 | 119 | 15982.378 | 110.625 | 15688 | 16187 | 0.007 |
| Harmonic 4 | 119 | 19879.647 | 110.643 | 19590 | 20112 | 0.006 |
| "*Colostethus*" cf. *ruthveni* | | | | | | |
| Call duration (s) | 23 | 2.391 | 0.340 | 1.848 | 3.086 | 0.142 |
| Notes per call | 23 | 21 | 4 | 15 | 29 | 0.182 |
| Rate of notes per second (notes/s) | 23 | 8.673 | 0.760 | 7.607 | 9.713 | 0.088 |
| Note duration (s) | 478 | 0.029 | 0.005 | 0.017 | 0.083 | 0.183 |
| Internote interval (s) | 455 | 0.090 | 0.016 | 0.056 | 0.189 | 0.179 |
| Dominant frequency (Hz) | 478 | 4909.584 | 279.119 | 4180 | 5307 | 0.057 |

show ascending frequency modulation, with a mean dominant frequency of 5,069.847 Hz (SD = 377.427 Hz). Notes have one to four visible harmonics at 7,648.673 Hz (SD = 581.536 Hz), 9,594.842 Hz (SD = 611.093 Hz), 12,680.165 Hz (SD = 456.792), and 14,970.233 Hz (SD = 345.457 Hz). When evaluating the variation of each call trait of "*C.*" *ruthveni* sensu stricto, it is evident that the dominant frequency was the only almost static feature (CV = 0.074), while the others showed a considerable variation (CV > 0.3).

The AC of "*Colostethus*" sp. *ruthveni*-like differs considerably from the AC of "*Colostethus*" *ruthveni* sensu stricto by its lower dominant frequency (mean = 4,301.160 Hz, SD = 90.273 Hz) and shorter notes (mean = 0.025, SD = 0.010 s). All analyzed notes show four visible harmonics at 8,196.504 Hz (SD = 104.165 Hz), 12,091.546 Hz (SD = 109.780 Hz), 15,982.378 Hz (SD = 110.625 Hz), and 19,879.647 Hz (SD = 110.643 Hz). The AC of "*C.*" cf. *ruthveni* differs from those previously mentioned by its higher rate of notes per second (mean = 8.673 notes/s, SD = 0.760 notes/s) and its shorter internote intervals (mean = 0.090 s, SD = 0.016 s). None of the ACs of "*C.*" cf. *ruthveni* showed visible harmonics.

### Courtship call

The description of the CC of "*Colostethus*" *ruthveni* sensu stricto was based on four calls of one male. This vocalization consists of a short squeak with partially fused pulses and modulated amplitude (Fig. 6). The mean duration of the CC is 0.124 s (SD = 0.038 s, range = 0.077–0.293 s) with a frequency between 4,415–12,300 Hz and a mean dominant frequency of 4,706.6 Hz (SD = 252.204 Hz, range = 4,489–5,093 Hz). Harmonics are not visible. The CC is followed by a silence interval with a mean duration of 0.566 s (SD = 0.525, range = 4,489–5,093 Hz) before the AC starts.

## Discussion

### Advertisement call

All call traits evaluated for the members of the "*Colostethus*" *ruthveni* group differed among the basins. Although the effect of ambient temperature and male size could not be evaluated, it can be assumed that all the variation produced by these external variables is summarized in the CVs calculated for each call trait in each basin. The variation in the ACs of allopatric populations may be due to potentially different environmental conditions (Köhler et al. 2017). For example, clinal variations have been described in the ACs of other dendrobatoids, such as *Rheobates palmatus* (Werner, 1899) from the Eastern Andes of Colombia (Bernal et al. 2005) and *Oophaga pumilio* (Schmidt, 1857) from Central America (Pröhl et al. 2007). On the other hand, early intrapopulation divergence has been evidenced in *O. granulifera* (Taylor, 1958) from Costa Rica, where two lineages show acoustic differentiation (Brusa et al. 2013). The acoustic differentiation of "*C.*" *ruthveni* sensu stricto and "*C.*" sp. *ruthveni*-like is congruent with the morphological and genetic divergence (Rueda-Almonacid et al. 2008, Grant et al. 2017). Therefore, the hypothesis that northwestern and southeastern populations of the "*C.*" *ruthveni* group are not conspecific is reinforced.

Advertisement calls of the members of the "*C.*" *ruthveni* group consist of a relatively long sequence of trills. However, this AC type is not present in the tribe Dendrobatini, the clade most closely related to the "*C.*" *ruthveni* group (Grant et al. 2017). In fact, the AC of members of the "*C.*" *ruthveni* group is more similar in structure (and to the human ear) to the AC of *Phyllobates* Bibron, 1840, aromobatids, colostethines, and hyloxalines. This supports that the trills have appeared several times in the evolutionary history of Dendrobatoidea (Lötters et al. 2003, Erdtmann & Amézquita 2009, Santos et al. 2014).

Comparisons of the ACs of the "*C.*" *ruthveni* group are limited by the few calls described for geographically close or morphologically similar species. In structure, the ACs of

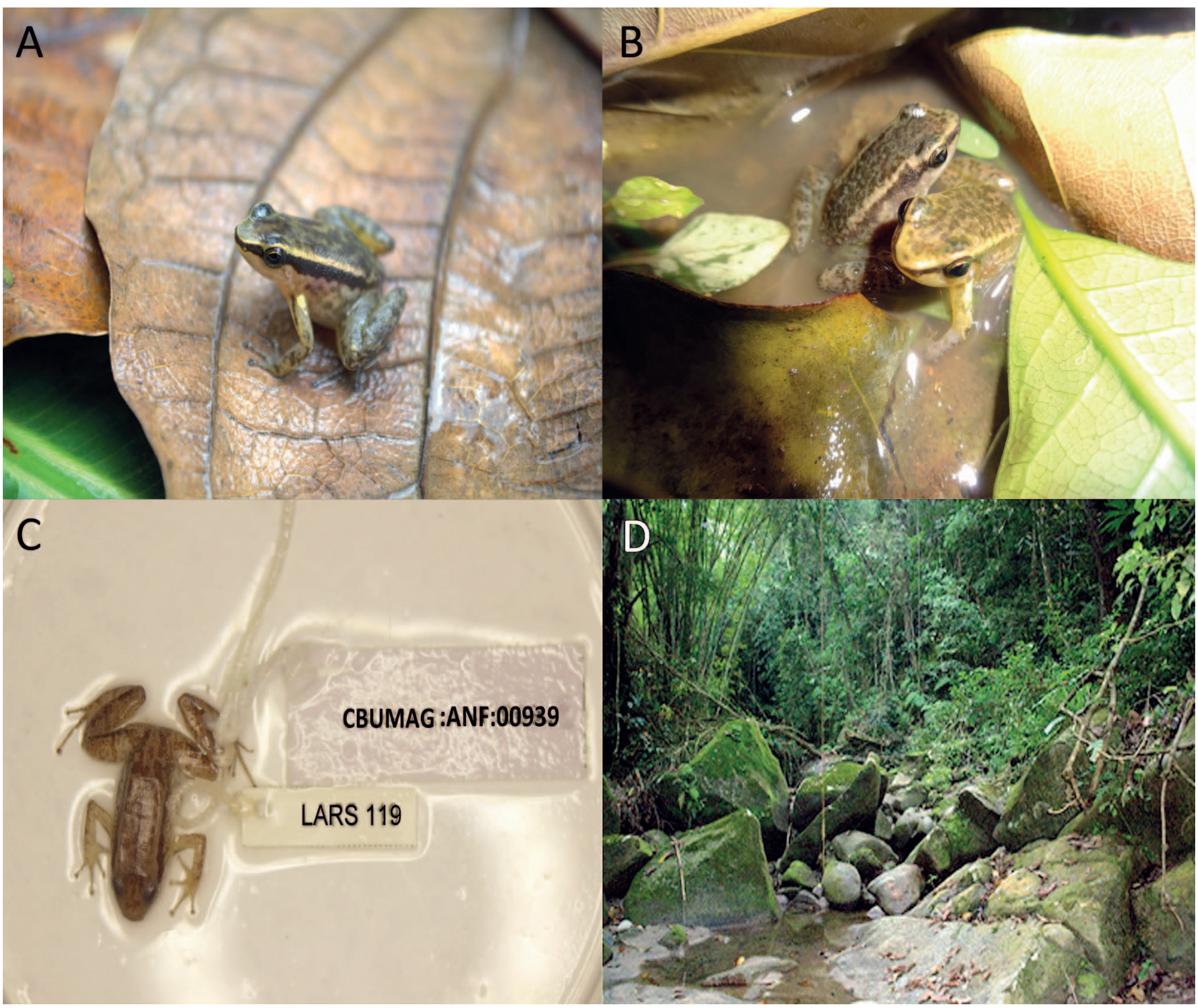


Figure 5. Specimens of the "*Colostethus*" *ruthveni* group. "*Colostethus*" *ruthveni* sensu stricto from Hacienda la Victoria, Santa Marta, Magdalena department (A). "*Colostethus*" sp. *ruthveni*-like from Donachuí Village, Valledupar, Cesar department (B). "*Colostethus*" cf. *ruthveni* from Wimangaga reserve, Dibulla, La Guajira department (C, specimen CBUMAG:ANF:00939). Small creek; typical habitat of members of the "*Colostethus*" *ruthveni* group (D).

these frogs are very similar to those of other trans-Andean dendrobatoids such as *Allobates talamancae* (Cope, 1875 "1876"), *A. ignotus* Anganoy-Criollo, 2012, *R. palmatus*, and *Colostethus panamensis* (Dunn, 1933). However, the dominant frequencies of *A. talamancae* (4,865–5,354 Hz, Lechelt et al. 2014) and *A. ignotus* (4,562–5,312 Hz, Granda-Rodríguez et al. 2018) exceed the dominant frequencies of "*C.*" sp. *ruthveni*-like (3,979–4,487 Hz) and "*C.*" cf. *ruthveni* (4,180–5,307 Hz), while they are slightly lower than the dominant frequency of "*C.*" *ruthveni* sensu stricto (4,177–5,944 Hz). In contrast, the dominant frequency of *R. palmatus* (2,700 Hz, Lüddecke 1999) is considerably lower than that of any member of the "*C.*" *ruthveni* group. The dominant frequency of *C. panamensis* (4,126–4,547 Hz, Wells 1980a) is similar to "*C.*" sp. *ruthveni*-like, but the frequency range is smaller than in "*C.*" *ruthveni* sensu stricto and "*C.*" cf. *ruthveni*. For other dendrobatoids with trans-Andean distribution, such as *Allobates niputidea* Grant, Acosta-Galvis & Rada, 2007, *A. wayuu* (Acosta-Galvis, Coloma & Cuentas, 1999), *Aromobates* aff. *saltuensis* (Rivero, 1980 "1978"), *A. tokuko* Rojas-Runjaic, Infante-Rivero & Barrio-Amorós, 2011, *Colostethus inguinalis* (Cope, 1868) and *Dendrobates truncatus* (Cope, 1861 "1860") (Acosta-Galvis et al. 1999, Grant 2004, Grant et al. 2007, Rojas-Runjaic et al. 2011, Anganoy-Criollo 2012, Gualdrón-Duarte et al. 2016), advertisement call descriptions of have not been published.

## Courtship call

The courtship call of "*Colostethus*" *ruthveni* sensu stricto is a squeaking noise, emitted only during the close encounter of males and females. This type of call differs considerably in structure from the AC in that it is much shorter but with longer partially fused notes, and a slightly lower dominant frequency. These characteristics have also been described for the CC of *Phyllobates bicolor* Bibron 1840, *Ameerega braccata* (Steindachner, 1864), *Allobates femoralis* (Boulenger, 1884 "1883") and *A. talamancae*. However, CCs of these species differ from those of "*C.*" *ruthveni* sensu stricto by their duration and dominant frequency (*P. bicolor*: 0.6 s, 2,375 Hz, Zimmerman & Zimmerman 1985; *A. braccata*: 0.043 s, 3,609.8–3,778.8 Hz, Forti et al. 2010; *A. femoralis*: without specific values, see spectrograms of Weygoldt 1980; *A. talamancae*: 0.2 s, 1,500–4,200 Hz, Kollarits et al. 2017).

Unlike in "*C*" *ruthveni* sensu stricto, the CCs of some dendrobatoids are not very different from their ACs. In some cases, the CC consists of a continuous sequence of trills, but with notes of a different shape from the typical AC, such as in *R. palmatus* (20 long notes, 2,000–2,800 Hz, Lüddecke 1999). Other species have a CC with similar notes to those of the AC, differing only in the number of notes per call and the rate of repetition. For example, *Mannophryne trinitatis* (Garman, 1888 "1887"), *Anomaloglossus stepheni* (Martins, 1989) and *Allobates marchesianus* (Melin, 1941) produce ACs composed of few notes, while the CCs consists of a longer sequence of similar notes, with lower (*A. stepheni*: AC = 7–8 notes per call, 4,600–4,800 Hz vs CC = 34 notes per call, 3,500–4,500 Hz, Juncá 1998) or equal (*M. trinitatis*: 2 notes per call vs 3–27 notes per call, 4,300–4,600 Hz, Wells 1980b, La Marca 1994; *A. marchesianus*: 1 note per call vs 30 notes per call, 4,500–7,000 Hz, Juncá 1998) dominant frequencies.

In general, anurans have a lower dominant frequency in the CC as compared to the AC (Toledo et al. 2015). However, there are particular cases such as *Anomaloglossus beebei* (Noble, 1923), where the CC and the AC have the same structure (note triplets), but the dominant frequency of the AC is higher than that of the CC (4,630–5,730 Hz vs 3,750–4,590 Hz, Pettit et al. 2012). On the other hand, some species such as *Hyloxalus toachi* (Coloma, 1995) present two types of CCs, which have dominant frequencies in the same range (4,000–4,300 Hz) and the same note structure as in the AC, but differ in the number of notes per call and

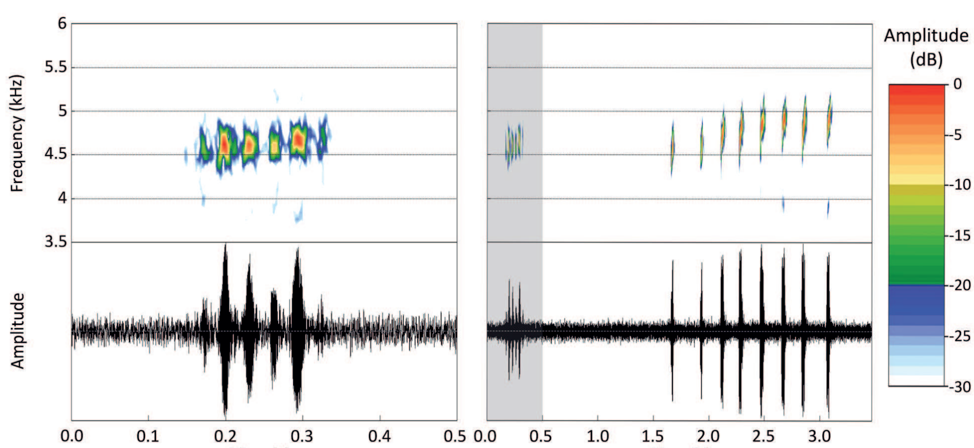


Figure 6. Courtship call of "*Colostethus*" *ruthveni* sensu stricto from Arimaca, Marinca Creek, Minca Village, Gaira basin. Half-second fragment (left) and full recording including subsequent advertisement call (right). Grayish area shows the half-second fragment within the full recording.

the rate of repetition (AC = 10–51 notes per call, two calls per minute; CC1 = 32–72 notes per call, one call per minute; CC2 = 1–2 notes per call, 1–6 calls per minute, Quiguango-Ubillús & Coloma 2008). Although the CC is poorly known in anurans in general, the scarce literature available shows that dendrobatoids present highly diversified CCs, probably related to the complexity of social behavior described for these frogs (Dole & Durant 1974, Wells 1980a, b, Wells 2007).

## Taxonomic remarks

To restrict the populations from the northwestern sector of the SNSM as "*Colostethus*" *ruthveni* sensu stricto, the following aspects were taken into account: (1) Viernes Santo creek is a tributary of the Toribio river, (2) most of the type series (14 of 16 specimens) described by Kaplan (1997) come from the Gaira and Toribio basins, (3) Gaira, Toribio and Los Rodríguez basins are the geographically closest basins, (4) there are no obvious morphological differences (sensu Kaplan 1997) between specimens coming from these basins.

Unfortunately, we were unable to obtain specimens from Donachuí (upper Cesar basin). Nevertheless, males recorded in this locality are morphologically very similar to specimens from Pueblo Bello (33.9 km southwest of Donachuí) and Atanquez (11.7 km east of Donachui), two villages of Valledupar (Cesar department). Males from Donachuí, Pueblo Bello, and Atanquez coincide in an exceptional character of sexual dimorphism, with a darker coloration of the gular region (absent in males of "*C.*" *ruthveni* sensu stricto). This character was described by Rueda-Almonacid et al. (2008) for "*C.*" sp. *ruthveni*-like (as "*Allobates* sp.") from Los Besotes. Results of the PCA agree with the hypothesis on the divergence between "*C.*" *ruthveni* sensu stricto and "*C.*" sp. *ruthveni*-like proposed by Grant et al. (2017). Certainly, the specimens of "*C.*" *ruthveni* reported from Nabusímake (Anganoy-Criollo 2012, Granda-Rodríguez et al. 2014) also correspond to "*C.*" sp. *ruthveni*-like.

Populations of the "*Colostethus*" *ruthveni* group from the northern sector of SNSM are still poorly known. We consider the specimens from Ancho river basin as "*C.*" cf. *ruthveni* by their acoustic differences, and the considerable geographic distance to "*C.*" *ruthveni* sensu stricto. Furthermore, for two specimens from Wimangaga reserve, middle Ancho river basin, Dibulla, La Guajira department, the disc of toe V does not reach the anterior border of the middle subarticular tubercle of the toe IV when toes are adpressed (at the same level in "*C.*" *ruthveni* sensu stricto). Nevertheless, additional specimens from the basin are required, to determine if this condition is a consequence of the state of preservation of the specimens or if it represents a morphological character established in this population.

A detail that requires clarification is the geographic localization of the "Mountains west [or east] of San Miguel and Don Diego", a locality where two paratypes of "*C.*" *ruthveni* were collected (Ruthven 1922, Kaplan 1997). Although Rivero (1963, foot note, p. 119) mentioned that San Miguel and Don Diego are not the same place, several subsequent publications referred to these sites as being the same or very close localities situated in the Magdalena department (Ruiz-Carranza et al. 1994, Kaplan 1997, Granda-Rodríguez et al. 2014). However, Don Diego is a coastal town (at sea level) located at the mouth of the homonymous basin, northern sector of the SNSM, Santa Marta, Magdalena department. No members of the "*C.*" *ruthveni* group have so far been reported from this site, although a distribution in the middle basin of the Don Diego River is very likely. On the other hand, San Miguel is an indigenous town located in mid-altitudes (1,600 m a.s.l.) in the northern sector of the SNSM, on the Macotama Creek, a tributary of the Ancho river in its upper basin, Dibulla, nowadays in La Guajira department. Although we could not review the type series of the species, the paratypes from Ancho basin probably also correspond to "*C.*" cf. *ruthveni*.

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## Appendix

Examined specimens

*"Colostethus" ruthveni* sensu stricto: COLOMBIA. Magdalena department: Santa Marta: Gaira river basin: corregimiento de Minca (CBUMAG:ANF:00253), Hacienda La Victoria (CBUMAG:ANF:00253, 527, 547–548, 551, 555–557, 560–562, 567–568, 662); Toribio river basin: vereda Bella Vista (CBUMAG:ANF:00222); Los Rodríguez creek basin: vereda Las Tinajas (CBUMAG:ANF:00752–757). "*Colostethus*" sp. *ruthveni*-like: COLOMBIA. Cesar department: Valledupar: corregimiento de Pueblo Bello (CBUMAG:ANF:891)."*Colostethus* cf. *ruthveni*: COLOMBIA. La Guajira department. Dibulla: Reserva Wimangaga (CBUMAG:ANF:00939, 944, 948).

**Supplementary material**

Raw data and data of statistical analyses.