

Review of the taxonomy and conservation status of the Ecuadorian Glassfrog *Centrolenella puyoensis* Flores & McDiarmid (Amphibia: Anura: Centrolenidae)

DIEGO F. CISNEROS-HEREDIA¹ & ROY W. MCDIARMID²

¹College of Biological and Environmental Sciences, Universidad San Francisco de Quito, Casilla Postal 17-12-841, Quito, Ecuador; and, 2002 Research Training Program, National Museum of Natural History, Smithsonian Institution. E-mail: diegofrancisco@cisneros-heredia.org

²US Geological Survey, Patuxent Wildlife Research Center, National Museum of Natural History, Room 378, MRC 111, Washington, DC 20013-7012 USA. E-mail: mcdiarmr@si.edu

Abstract

The Glassfrog *Centrolenella puyoensis* Flores & McDiarmid is a taxon known only from the female holotype, and recently placed in the genus *Centrolene* due to its supposed close relationship with *Centrolene mariaae* (Duellman & Toft). Herein we report new material of *puyoensis*, including adult male specimens previously unknown. We propose the new combination *Cochranella puyoensis* (Flores & McDiarmid) n. comb., in recognition of the state of the humeral *crista ventralis* in males of this species, which lack a humeral spine. The hypothesis of relationships between three species, including *puyoensis*, proposed as the *mariaae* species-group is questioned as it was based on phenetic rather than derived characters. We present new data that extend the distributional range of *Cochranella puyoensis*, and define its range along the Foothill Evergreen forests from 400 m to 1000 m above sea level in the provinces of Napo, Orellana, and Pastaza. New data presented herein also permit a re-evaluation of the conservation status of the species, previously classified under the IUCN category of Critically Endangered. We recommend that *Cochranella puyoensis* be reclassified as “Endangered”: EN B1ab(i,ii,iii)+2ab(i,ii,iii); based on a better understanding of the presence of the species, its occupancy area, number of known localities, and habitat quality status.

Key words: *Cochranella puyoensis* n. comb., distributional range, conservation status, Ecuador

Resumen

La Rana de Cristal *Centrolenella puyoensis* Flores & McDiarmid es un taxón conocido solamente del espécimen holotipo hembra y recientemente ubicado en el género *Centrolene* debido a su supuesta relación cercana con *Centrolene mariaae* (Duellman & Toft). Nosotros reportamos nuevo material de *puyoensis* incluyendo especímenes machos adultos previamente desconocidos. Proponemos la nueva combinación *Cochranella puyoensis* (Flores & McDiarmid) n. comb., en

reconocimiento del estado de la *crista ventralis* del húmero de los machos de esta especie, que carece de una espina humeral. La hipótesis de relaciones entre tres especies, entre ellas *puyoensis*, propuesta como el grupo-de-especies *mariae* es cuestionada debido a que se basó en caracteres fenéticos y no derivados. Presentamos nuevos datos que extienden el rango de distribución de *Cochranella puyoensis* y definimos su rango en los bosques Siempreverdes Piemontanos ubicados entre 400 m a 1000 m sobre el nivel del mar en las provincias de Napo, Orellana y Pastaza. Los nuevos datos presentados aquí también permiten una re-evaluación de estado de conservación del la especie, previamente clasificada bajo la categoría IUCN de Peligro Crítico (CR). Recomendamos que *Cochranella puyoensis* se re-clasifique como “En Peligro”: EN B1ab(i,ii,iii)+2ab(i,ii,iii); basados en un mejor entendimiento de la extensión de presencia de la especie, su área de ocupación, el número de localidades conocidas y el estado de la calidad del hábitat.

Palabras clave: *Cochranella puyoensis* n. comb., rango de distribución, estado de conservación, Ecuador

Introduction

The family Centrolenidae (Amphibia: Anura) currently includes four genera: *Allophryne*, *Centrolene*, *Cochranella*, and *Hyalinobatrachium* (Ruiz-Carranza & Lynch 1991, Frost *et al.* 2006). *Centrolene* and *Cochranella* are distinguished from each other by the state of a single sexually-dimorphic character: presence of humeral spines in males. Consequently, taxa known only from females are problematic regarding its generic assignment (Flores & McDiarmid 1989; Ruiz-Carranza & Lynch 1991; Duellman & Schulte 1993). Three taxa, *Centrolenella mariae* Duellman & Toft, 1979, *Centrolenella azulae* Flores & McDiarmid, 1989, and *Centrolenella puyoensis* Flores & McDiarmid, 1989, were described from female type specimens, and all are known only from their type localities in the eastern slopes of the Andes of Ecuador and Peru. Flores and McDiarmid (1989) hypothesized that these three species formed a monophyletic group (the *mariae* species group) based on several characters that they thought were shared and derived among the centrolenids. When Ruiz-Carranza and Lynch (1991) proposed a new generic arrangement within Centrolenidae, they included *mariae*, *azulae* and *puyoensis* into the genus *Cochranella*. Duellman and Schulte (1993) subsequently transferred *mariae* to the genus *Centrolene* — based on M. Hensel’s comment about humeral spines in males of *mariae*. Duellman and Schulte (1993) also placed *azulae* and *puyoensis* in the genus *Centrolene*, following Flores and McDiarmid’s (1989) hypothesis. This action was followed by Ruiz-Carranza and Lynch (1995a), but these authors stated that the similarities between those taxa were phenetic and not based on derived characters.

In the course of our research to understand the diversity and distribution of frogs of the family Centrolenidae, we found several specimens assignable to *Centrolenella puyoensis* that allow us to reassess the relationships of the species. The goals of this paper are to present our conclusions about the generic position, distribution, and conservation status of the Ecuadorian-endemic Glassfrog *Centrolenella puyoensis* Flores & McDiarmid, 1989.

Materials and methods

Most characters, terminology, and methods used herein follow the definitions of Ruiz-Carranza and Lynch (1991), and Cisneros-Heredia and McDiarmid (2006). The nuptial excrescences classification follows Flores' (1985) conventions. Snout-vent length is abbreviated in the text as SVL. Sex was determined by noting the presence or absence of secondary sexual characters (vocal slits, nuptial pads) and by direct observation of the gonads. Classification of vegetation formations in Ecuador follows Sierra (1999), and that of the zoogeographic zones follows Albuja *et al.* (1980). The geographic placement and elevation at collection localities were determined using collector's field notes and museum records and revised in accord with the 2000 physical map of the Republic of Ecuador (1:1'000000) distributed by the Instituto Geográfico Militar of Ecuador.

To assess the conservation status of *C. puyoensis* in Ecuador, we used the concepts established by the International Union for Conservation of Nature and Natural Resources — IUCN (IUCN 2001), including the terms “extension of presence” and “occupancy area”, and adopted the categories, criteria, and sub-criteria used for the classification of threatened species. The IUCN Red List Categories and Criteria are intended to be an easily and widely understood system for classifying species at high risk of global extinction (IUCN 2001). The criteria can be applied to any taxonomic unit and within any specified geographical or political area. Listing in a higher extinction risk category implies a higher expectation of extinction, and over the time-frames specified more taxa listed in a higher category are expected to go extinct than those in a lower one (without effective conservation action) (IUCN 2001). There are nine categories inside the IUCN (2001): Extinct — EX, when there is no reasonable doubt that the last individual has died; Extinct in the Wild — EW, when it is known only to survive in cultivation, in captivity or as a naturalized population well outside the past range; Critically Endangered — CR, when the best available evidence indicates that it meets any of the criteria (A to E) for the category and thus it is facing an extremely high risk of extinction in the wild; Endangered — EN, when the best available evidence indicates that it is facing a very high risk of extinction in the wild; Vulnerable — VU, when the best available evidence indicates that it is facing a high risk of extinction in the wild; Near Threatened — NT, when it has been evaluated against the criteria but does not qualify for Critically Endangered, Endangered or Vulnerable now, but is close to qualifying for or is likely to qualify for a threatened category in the near future; Least Concern — LC, when it has been evaluated against the criteria and does not qualify for Critically Endangered, Endangered, Vulnerable or Near Threatened; widespread and abundant taxa are included in this category; Data Deficient — DD, when there is inadequate information to make a direct, or indirect, assessment of its risk of extinction based on its distribution and/or population status; Not Evaluated — NE, when it has not yet been evaluated against the criteria (IUCN 2001). All taxa listed as Critically Endangered qualify for Vulnerable and Endangered, and all listed as Endangered qualify for Vulnerable. Together these categories are described as 'threatened'. For listing

as Critically Endangered, Endangered or Vulnerable there is a range of quantitative criteria; meeting any one of these criteria qualifies a taxon for listing at that level of threat. The criteria used for evaluation are: (A) Reduction in population size, (B) Geographic range in the form of extent of occurrence or area of occupancy, (C) and (D) Estimated population size, under different parameters, and (E) Quantitative analysis (IUCN 2001).

Institutional abbreviations used are as follow: USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA; QCAZ, Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador; DFCH-USFQ, Universidad San Francisco de Quito, Quito, Ecuador. Examined material: *Centrolenella puyoensis*: Ecuador: DFCH-USFQ D285, ca. 45 km E of Narupa, on the Hollín–Loreto road (ca. 800 m), province of Napo, collected by D. F. Cisneros-Heredia, C. Schneider, and J. Fabara on 06 November 1999; QCAZ 7104, 7499, Río Huataracu, ca. 70 km E of Hollín, on the Hollín–Loreto road (ca. 400 m), province of Orellana, collected by F. Campos, L. Coloma, and J.-M. Touzet on 15 January 1995; USNM 291298, “Río Pucayacu”, province of Pastaza, collected by Ramon Olalla. *Centrolene azulae*: Peru: USNM 195988 (holotype): Cordillera Azul, department of Huánuco. *Centrolene mariae*: Peru: KU 174713: Serranía de Sira, department of Huánuco. *Cochranella cochranae*: Ecuador: USNM 284304–6, 286632–36: Cascada de San Rafael, province of Napo; USNM 288452: near Loreto, province of Orellana; DFCH D100-1: Contrafuerte de Tzunantza, province of Zamora-Chinchipe; FHGO 2804: Romerillos, province of Zamora-Chinchipe.

Results

Centrolenella puyoensis has not been reported in the literature since the type description by Flores and McDiarmid (1989), except for its inclusion in checklists (Almendáriz 1991, Coloma 1991, Frost 2004, Coloma 2005–2006). We have examined four additional specimens of this glassfrog collected on the central eastern Andean slopes of Ecuador. All specimens (DFCH-USFQ D285, QCAZ 7104, QCAZ 7499, and USNM 291298) have the distinctive color pattern and morphological features described for *Centrolenella puyoensis* by Flores and McDiarmid (1989).

Information on coloration in life is available for QCAZ and DFCH-USFQ specimens and agrees well with the description of *Centrolenella puyoensis*: light green dorsum with light yellow or cream spots, light green flanks, white line on upper lip, white parietal peritoneum, green bones (QCAZ archive, D. F. Cisneros-Heredia field notes). The coloration in preservative varies from dark to pale purplish-grey with clear spots; the bones are mostly white, except for a green shadow still visible in the knees even in the older USNM specimen. Two specimens (DFCH-USFQ D285, QCAZ 7104) have slight differences in the form of the snout; in these, the snout is truncate in profile instead of round as described and illustrated for the holotype. The USNM specimen has the snout slightly crushed but in all other characters, it coincides with *Centrolenella puyoensis*.

The anal ornamentation pictured by Flores and McDiarmid (1989) is present in some specimens (USNM 291298) but barely evident in others (DFCH-USFQ D285, QCAZ 7104). This ornamentation does not seem to be related to the sex of the specimens, as both males and females show it, and the variation is probably due to age or preservation artifacts. All specimens of *Centrolenella puyoensis* have the characteristic microgranulations on the dorsal skin described by Flores and McDiarmid (1989).

Two specimens (DFCH-USFQ D285, QCAZ 7499) are adult females, and two specimens (QCAZ 7104, USNM 291298) are adult males. The male specimens are the first reported for *Centrolenella puyoensis*, previously known only from the female holotype. Both male specimens (QCAZ 7104, USNM 291298) are similar in most features to females; however, males are smaller than females (21.2–25.4 mm SVL in males, 27.2–30.0 mm SVL in females), have vocal slits extending from the angles of the jaws to a point midway along the base of the tongue, an enlarged prepollex (but without an externally protruding prepollical spine or bulge), type-I nuptial pads at the base of the thumb (present in USNM 291298, although difficult to see without proper light conditions), and have conical tubercles on the top of the head, in the loreal region, and on the flanks. Both male specimens (QCAZ 7104, USNM 291298) lack humeral spines or humeral crests.

Discussion

Taxonomic status

The genus *Centrolene* is currently delimited only by the presence of a single synapomorphy, humeral spines in adult males. The genus *Cochranella* is defined only by the absence of such humeral spines (Ruiz-Carranza & Lynch 1991; Frost *et al.* 2006). Frost *et al.* (2006) suggested that coding this character just as presence/absence is simplistic, as much more variation is observed in both genera; (e.g., *Centrolene geckoideum* Jiménez de la Espada, 1872 has a sharp, smooth, protruding humeral spine in males, and a poorly developed, non-protruding humeral spine in females; *Centrolene prosoblepon* (Boettger, 1892) has a blunt, bladelike, projecting humeral spine in males; and *Cochranella griffithsi* (Goin, 1961) has a bladelike, irregular, non-projecting humeral crest [Frost *et al.* 2006, Cisneros-Heredia & McDiarmid unpubl. data]). Further, both genera, *Centrolene* and *Cochranella*, are currently recognized as non-monophyletic units (Darst & Cannatella 2004; Frost *et al.* 2006).

Although we recognize the current limitations of the generic classification of Centrolenidae, we proposed the following new combination for *Centrolenella puyoensis* to recognize the state of the humeral *crista ventralis* in males of this species, i.e., lacking a humeral spine or blade-like humeral crest.

Cochranella puyoensis (Flores & McDiarmid, 1989) n. comb.

Centrolenella puyoensis Flores and McDiarmid, 1989: *Herpetologica*, 45(4), 406 [original description]. Holotype: MCZ 91187, type locality: "1.0 km W Puyo, Provincia de Pastaza, Ecuador, between 1000–1050 m elevation". Coloma, 1991: 13 [list of Ecuadorian amphibians]. Almendáriz, 1991: *Politécnica*, XVI (3), 96 [list of Ecuadorian herpetofauna].

Cochranella puyoensis — Ruiz-Carranza and Lynch, 1991: *Lozania*, 57: 23 [new combination under *Cochranella*].

Centrolene puyoensis — Duellman and Schulte, 1993: *Occas. Pap. Mus. Nat. Hist. Univ. Kansas*, 155, 1–33 [new combination under *Centrolene*]. Cisneros-Heredia and McDiarmid (2006): *Zootaxa*, 1244, 1–32 [analysis of Glassfrogs from eastern Ecuador].

Centrolene puyoense — Frost, 2004: *Amphibian Species of the World: Online* [changed for gender agreement]. Coloma and Ron, 2004: *IUCN Red List of Threatened Species: online* [threatened status]. Coloma, 2005–2006: *Anfibios de Ecuador: online* [list of Ecuadorian amphibians].

In order to provide future workers with data useful in characterizing *Cochranella puyoensis*, a numbered diagnosis is provided: (1) vomerine teeth present; (2) bones green in life; white or whitish green in preservative; (3) parietal peritoneum covered by guanophores (white), extending posteriorly to the level of the liver and covering the upper half of the stomach; visceral peritoneum clear; (4) coloration in life dark to light green dorsally with small yellow to cream spots/specks, venter bluish-green; in preservative dark to pale purplish-grey with light spots; (5) webbing formula of hand: webbing absent between I and II and vestigial between II and III, III (3⁻–3) – (2_{1/2}–2_{2/3}) IV; (6) webbing formula of foot: I (2–2⁻) – (2_{1/3}–2_{1/2}) II 1_{1/2}–2⁻ III (1_{1/2}–1_{2/3}) – 2_{2/3} IV (2⁺–2_{2/3}) – (1_{2/3}–2⁻) V; (7) snout truncate in dorsal view and truncate to rounded in profile; nostrils slightly elevated and separated by a shallow depression; loreal region concave; (8) all skin surfaces with minute granulations, dorsal skin with scattered low warts or spicules; (9) low non-enameled ridge on forearms and hand; unscaloped fold on tarsus; (10) humeral spine absent in males; (11) tympanum evident ventrally, upper 1/4 to 1/3 concealed, directed dorsolaterally with slight posterior inclination; supratympanic fold moderately developed to barely evident; (12) 21.2–25.4 mm SVL in males, 27.2–30.0 mm SVL in females; (13) prepollical spine not protruding externally; unpigmented nuptial pad Type I; (14) anal ornamentation with at least two paired tubercles below vent and some additional tubercles and folds; (15) first finger longer than second; (16) lobate liver without guanophores; (17) eye diameter larger than width of disc on finger III; (18) iris in life light blue-green with a transverse green-brown bar (holotype, DFCH-USFQ D285, QCAZ 7104) or white with grey-green fine reticulations and a transverse gray bar (QCAZ 7499), iris in preservative grey with some fine dark reticulations, minute dark punctuations, and a transverse dark grey bar; (19) some melanophores on fingers and toes; (20) advertisement call unknown.

The absence of a humeral spine in *C. puyoensis* would present a contradiction for the hypothesized relationships with *C. mariae* (Flores & McDiarmid 1989), because *C. mariae* was reported to have humeral spines (M. Hensel, pers. comm., in Duellman and Schulte 1993: 31). Unfortunately, no voucher specimens of males of *mariae* have been studied or reported to be deposited in collections, and the state of the humeral *crista ventralis* (either with or without a humeral spine) has not been corroborated. The coloration patterns of *puyoensis*, *mariae* and *azulae* are similar and, to the best of our knowledge, unique among glassfrogs (only *C. ocellata* has a similar coloration pattern, and we think that it is probably related to *C. puyoensis*), but without a phylogeny of Centrolenidae any conclusion about their relationships is speculative at best and dependent on the collection and examination of male specimens of *mariae* and *azulae*. If *mariae* and *puyoensis* are closely related, their placement in different genera would be a consequence of the non-monophyly nature of the centrolenid genera *Cochranella* and *Centrolene* (and the non-informative nature of the character used to separate them: humeral spines) or to *C. mariae* actually lacking humeral spines, and Hensel's comments based on a male of a different species.

The conclusions by Flores and McDiarmid (1989) on the relationships between *puyoensis*, *mariae* and *azulae* (= *mariae* species group) were based on several characters considered synapomorphies (e.g., microgranulations on the skin surfaces, reduced interdigital webbing). Most subsequent authors have followed their hypothesis (Ruiz-Carranza & Lynch 1991; Duellman & Schulte 1993). Ruiz-Carranza and Lynch (1995a) were the first authors to suggest that the proposed *mariae* group was based on phenetic rather than derived characters, and we concur. The skin microgranulations were considered a unique character uniting *C. azulae*, *C. mariae*, and *C. puyoensis*, but we have subsequently found them present also in *C. cochranae* (Goin, 1961), *C. posadae* (Ruiz-Carranza & Lynch, 1995a), *C. luminosa* (Ruiz-Carranza & Lynch, 1995b), *C. luteopunctata* (Ruiz-Carranza & Lynch, 1996), and *C. chami* (Ruiz-Carranza & Lynch, 1995b)—and they probably occur in more centrolenid species. Reduced webbing between the outer fingers is a condition present in several species of *Cochranella*. The particular combination of reduced hand webbing and presence of vomerine teeth is present in *Cochranella chami*, *C. cochranae* (some specimens), *C. cristinae* (Ruiz-Carranza & Lynch, 1995b), *C. luminosa*, *C. luteopunctata*, *C. prasina* (Duellman, 1981), *C. puyoensis*, and *C. spilota* (Ruiz-Carranza & Lynch, 1997).

Conservation status

New data presented herein extend the distributional range of *Cochranella puyoensis*. All records from the provinces of Napo and Orellana are located in the Huataracu River Basin, ca. 100 km NE from the type locality (1 km W of Puyo). We think that the locality of the specimen reported from “Río Pucayacu” (USNM 291298) corresponds to some place in the Andean foothills in the Upper Bobonaza River Basin, province of Pastaza, and

not to the mouth of the Pucayacu River near Montalvo (c. 315 m elevation) mentioned in the Ecuadorian gazetteer of Paynter (1993). The Pucayacu River near Montalvo is located in the Amazonian lowlands region of the province of Pastaza (Paynter 1993), while *Cochranella puyoensis* is a species from foothill regions. The highest elevational record of *Cochranella puyoensis* is about 1,000 m elevation at the type locality (1 km W of Puyo, province of Pastaza); and the lowest point is around 400 m elevation, in the Huataracu River Basin. All records of *C. puyoensis* are localities within the provinces of Napo, Orellana, and Pastaza, Ecuador, and this taxon is apparently restricted (endemic) to the Foothill Evergreen forests of the central section of the eastern Andean slopes of Ecuador, in the Eastern Subtropical zoogeographic zone (Fig. 1).

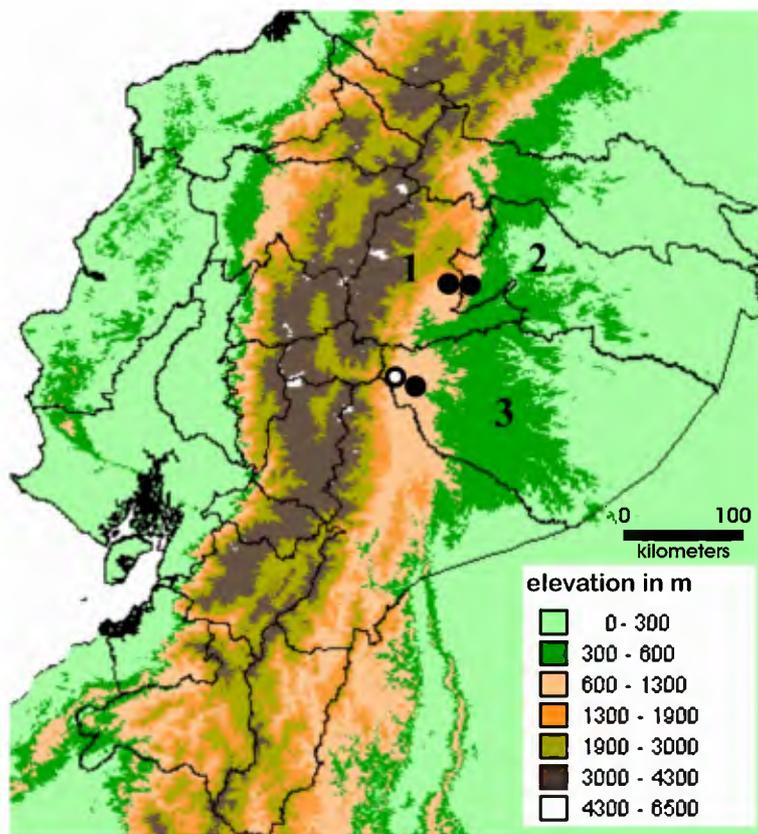


FIGURE 1. Distribution of the Glassfrog *Cochranella puyoensis* (Flores and McDiarmid) in Ecuador. Circle corresponds to the type locality, 1.0 km W Puyo (province of Pastaza = 3), and dots to new localities reported herein: ca. 45 km E of Narupa (province of Napo = 1), Río Huataracu (province of Orellana = 2), “Río Pucayacu” (province of Pastaza = 3).

Cochranella puyoensis was classified as “Critically Endangered” by Coloma and Ron (2004) because “its extent of occurrence is less than 100 km², all individuals are in a single location, and there is continuing decline in the extent and quality of its habitat around the

city of Puyo [city incorrectly cited as “Douala” in Coloma & Ron 2004]”. However, new data presented herein led us to reconsider its conservation status. *Cochranella puyoensis* is more widely distributed than previously thought and now it is known to occur in two separate areas: the region around Puyo and two localities on the southeastern slope of Volcan Sumaco in the Huataracu River drainage (Fig. 1). This species is still restricted to just one vegetation formation, the Foothill Evergreen forests of eastern Ecuador. This vegetation formation had a historical area of ca. 13,200 km². Today ca. 38 % has been severely affected by anthropogenic activities with ca. 8,200 km² remaining (Sierra *et al.*, 1999 with data from 1996). Moreover, ca. 55% (ca. 4,500 km²) of the remaining forest is less than 3 km from zones of high human pressure (e.g. deforestation, uncontrolled extension of the agricultural frontier, water pollution), and only ca. 10% of the remaining Foothill Evergreen forests is protected inside the Ecuadorian Protected Areas System (SNAP) (Sierra *et al.*, 1999). As with nearly all species of centrolenid frogs, *Cochranella puyoensis* presumably reproduces along rivulets in primary or secondary forests, it does not persist in heavily impacted areas such as pastures. Thus, its occupancy area is probably even less than the 8,200 km² of remaining potentially habitat (extension of presence), and closer to 3,700 km² (remaining suitable habitat, at more than 3 km from zones of high human pressure).

Because the current extension of presence of *Cochranella puyoensis* is less than 5,000 km² but larger than 100 km² (criteria B1), its occupancy area is probably less than 500 km² but larger than 100 km² (B2), it is known from fewer than five localities (criteria B1a, B2a), population declines have been reported in several centrolenid species from the eastern slopes of Ecuador (criteria B1b, B2b) (Cisneros-Heredia & McDiarmid, 2005, Cisneros-Heredia *et al.* 2006); and, important considerations relative to its conservation status (extension of presence, occupancy area, and habitat quality) continue to decline (both observed and projected), we recommend that *Cochranella puyoensis* be treated as an “Endangered” species on both a national and global level under the IUCN (2001) system with the following criteria and sub-criteria: EN B1ab(i,ii,iii)+2ab(i,ii,iii).

Acknowledgments

For the access to specimens under their care, we thank Luis Coloma (QCAZ) and William Duellman (KU). DFCH is grateful to George Zug, Ronald Heyer, Robert Reynolds, Ken Tighe, Steve Gotte, Carole Baldwin, Mary Sangrey and Nina Buttler for their continuous support at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); to Jay Savage for useful discussions and help during the work on *C. puyoensis*; and to Janalee Caldwell for her kindness during DFCH stay at Oklahoma, where this paper was partially presented at the 2004 Joint Meeting of Ichthyologists and Herpetologists. We thank Luis Coloma, William Duellman, John D. Lynch, and Charles

Myers for their helpful comments, enlightened discussions, or provision of useful literature, and José Fabara and Chris Schneider for field companionship and support. DFCH express his deepest gratitude to the Smithsonian Women's Committee whose support allowed him to participate in the 2002 Research Training Program, National Museum of Natural History, Smithsonian Institution. Our studies of the Centrolenidae have been supported by the 2002 Research Training Program, National Museum of Natural History, Smithsonian Institution, the US Fish and Wildlife Service, the US Geological Survey, Universidad San Francisco de Quito, and María Elena and Laura Heredia.

References

- Albuja, L., Ibarra, M., Urgilés, J. & Barriga, R. (1980) *Estudio preliminar de los vertebrados ecuatorianos*. Departamento de Ciencias Biológicas, Escuela Politécnica Nacional, Quito.
- Almendáriz, A. (1991) Anfibios y reptiles. In: Barriga, R., Almendáriz, A. & Albuja, L. (Eds.), *Lista de Vertebrados de Ecuador*. Revista Politécnica, XVI (3), Quito, 89–162.
- Boettger, O. (1892) *Katalog der Batrachier-Sammlung in Museum der Senckenbergischen Naturforschenden Gesellschaft in Frankfurt am Main*. Frankfurt, 73 pp.
- Cisneros-Heredia, D.F. & McDiarmid, R.W. (2005) *Declining glassfrogs: Diversity and conservation status of the Centrolenidae from Ecuador*. Abstracts 2005 Joint Meeting of Ichthyologists and Herpetologists, Tampa, USA.
- Cisneros-Heredia, D.F. & McDiarmid, R.W. (2006) A new species of the genus *Centrolene* (Amphibia: Anura: Centrolenidae) from Ecuador with comments on the taxonomy and biogeography of Glassfrogs. *Zootaxa*, 1244, 1–32.
- Cisneros-Heredia, D.F., Guayasamin, J.M. & McDiarmid, R.W. (2006) *Declining populations of Ecuadorian Glassfrogs (Centrolenidae)*. Abstracts 2006 Joint Meeting of Ichthyologist and Herpetologists, New Orleans, USA.
- Coloma, L.A. (1991) *Anfibios del Ecuador: Lista de especies, ubicación altitudinal y referencias bibliográficas*. Reportes Técnicos 2, Ecociencia, Quito, 46 pp.
- Coloma, L.A. & Ron, S. (2004) *Centrolene puyoense*. In: IUCN, *IUCN Red List of Threatened Species*. IUCN, SSC Red List Programme, Cambridge. Available from: <http://www.redlist.org> (accessed on July 2006).
- Coloma, L.A. (2005-2006) Anfibios de Ecuador, Ver. 2.0. Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito. Available from: <http://www.puce.edu.ec/zoologia/vertebrados/amphibiawebec/index.html> (accessed July 2006).
- Darst, C.R. & Cannatella, D.C. (2004) Novel relationships among hylid frogs inferred from 12S and 16S mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, 31, 462–475.
- Duellman, W.E. (1981) Three new species of centrolenid frogs from the Pacific versant of Ecuador and Colombia. *Occasional Papers of the University of Kansas, Museum of Natural History*, 88, 1–9.
- Duellman, W.E. & Schulte, R. (1993) New species of centrolenid frogs from northern Perú. *Occasional Papers of the University of Kansas, Museum of Natural History*, 155, 1–33.
- Duellman, W.E. & Toft, C.A. (1979) Anurans from Serranía de Sira, Amazonian Perú: Taxonomy and biogeography. *Herpetologica*, 35 (1), 60–70.
- Flores, G. (1985) A new *Centrolenella* (Anura) from Ecuador, with comments on nuptial pads and prepollical spines in *Centrolenella*. *Journal of Herpetology*, 19 (3), 313–320.

- Flores, G. & McDiarmid, R.W. (1989) Two new species of South American *Centrolenella* (Anura: Centrolenidae) related to *C. mariae*. *Herpetologica*, 45(4), 401–411.
- Frost, D.R. (2004) Amphibian Species of the World. Version 3.0. American Museum of Natural History, New York, USA. Available from: <http://research.amnh.org/herpetology/amphibia/index.html> (accessed July 2006).
- Frost, D.R., Grant, T., Faivovich, J., Bain, R.H., Haas, A., Haddad, C.F.B., de Sa, R.O., Channing, A., Wilkinson, M., Donnellan, S.C., Raxworthy, C.J., Campbell, J.A., Blotto, B.L., Moler, P., Drewes, R.C., Nussbaum, R.A., Lynch, J.D., Green, D.M., & Wheeler, W.C. (2006) The amphibian tree of life. *Bulletin of the American Museum of Natural History*, 297, 1–370.
- Goin, C. (1961) Three new centrolenid frogs from Ecuador. *Zoologischer Anzeiger*, 166, 95–104.
- IUCN (2001) *IUCN Red List. Categories and Criteria*. Version 3.1. Gland, Cambridge, IUCN.
- Jiménez de la Espada, M. (1872) Nuevos batracios americanos. *Anales de la Sociedad Española de Historia Natural*, 1, 85–88.
- Paynter Jr., R.A. (1993) *Ornithological gazetteer of Ecuador*. Second Edition. Harvard College, 247 pp.
- Ruiz-Carranza, P.M. & Lynch, J.D. (1991) Ranas Centrolenidae de Colombia I. Propuesta de una nueva clasificación genérica. *Lozania*, 57, 1–30.
- Ruiz-Carranza, P.M. & Lynch, J.D. (1995a) Ranas Centrolenidae de Colombia V. Cuatro nuevas especies de *Cochranella* de la Cordillera Central. *Lozania*, 62, 1–23.
- Ruiz-Carranza, P.M. & Lynch, J.D. (1995b) Ranas Centrolenidae de Colombia VI. Cuatro nuevas especies de *Cochranella* de la Cordillera Occidental. *Lozania*, 63, 1–15.
- Ruiz-Carranza, P.M. & Lynch, J.D. (1996) Ranas Centrolenidae de Colombia IX. Dos nuevas especies del suroeste de Colombia. *Lozania*, 68, 1–11.
- Ruiz-Carranza, P.M. & Lynch, J.D. (1997) Ranas Centrolenidae de Colombia X. Los centrolénidos de un perfil del flanco oriental de la Cordillera Central en el Departamento de Caldas. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales*, 21 (81), 541–553.
- Sierra, R. (1999) *Propuesta Preliminar de un Sistema de Clasificación de Vegetación para el Ecuador Continental*. Proyecto INEFAN/GEF-BIRF EcoCiencia, Quito, 194 pp.
- Sierra, R., Campos, F. & Chamberlin, J. (1999) *Áreas prioritarias para la conservación de la biodiversidad en el Ecuador Continental*. Ministerio del Ambiente, Proyecto INEFAN/GEF-BIRF, EcoCiencia, WCS, Quito, 171 pp.