Natural history and intraspecific variation of the Ecuadorian Blue Glassfrog
Cochranella mache GUAYASAMIN & BONACCORSO, 2004
(Anura: Centrolenidae)

Biologie und innerartliche Variabilität des Ekuadorianischen Blauen Glasfrosches
Cochranella mache GUAYASAMIN & BONACCORSO, 2004
(Anura: Centrolenidae)

D. F. CISNEROS-HEREDIA & J. DELIA & M. H. YÁNEZ-MUÑOZ & H. M. ORTEGA-ANDRADE

ABSTRACT

We present new information on the natural history and intraspecific variation of Cochranella mache GUAYASAMIN & BONACCORSO, 2004. It is a nocturnal species associated with small streams across primary and old-secondary forests in the Cordillera Mache-Chindul, endemic to the Seasonal Evergreen forests of the West Ecuadorian Region. Intraspecific and sex-related variation is noted in several characters, including dorsal skin texture, expression of the dermal folds, cloacal ornamentation, expression of the supratympanic fold, and extent of iridophores on the hepatic peritoneum. Dramatic chromatic changes in life are reported, showing a unique pattern in Centrolenidae, its dorsal pattern changes from bluish-green with a dull yellow patch on the head and abundant yellow spots, to a lavender/light blue dorsum with a bright yellow patch on the head and abundant orange spots. In order to provide future researchers with useful information to characterize the species, we present a numbered diagnosis for Co. mache that includes all new information.

KEY WORDS
Amphibia: Anura: Centrolenidae; Cochranella mache; morphological variation, morphology, coloration; sexual dimorphism, systematics, biology, natural history; Ecuador

INTRODUCTION

The glassfrog Cochranella mache GUAYASAMIN & BONACCORSO, 2004 was described from three male specimens collected at one locality on the eastern slope of Cordillera Mache-Chindul (= Montañas de Mache), a rather isolated mountain range in the northern portion of Cordillera de la Costa in western, coastal Ecuador (GUAYASAMIN & BONACCORO 2004; CISNEROS-HEREDIA & MCDIARMID 2007). Cochranella mache is considered a threatened species and remains poorly understood (GUAYASAMIN 2007). Recent surveys carried out in the province of Esmeraldas, Ecuador, have yielded new information on Co. mache including data on aspects of its natural history and intraspecific variation, which we present herein.
MATERIALS AND METHODS

Characters and terminology follow definitions and proposals by Cisneros-Heredia & McDiarmid (2007). Terminology for the webbing formula follows the method of Savage & Heyer (1967) as modified by Savage & Heyer (1997) and latter summarized by Guayasamin et al. (2006) and Cisneros-Heredia & McDiarmid (2007). Sex was determined by direct examination of the gonads and by noting the presence of secondary sexual characters (i.e., vocal slits, nuptial pads). Internal anatomy was examined by dissection of recently euthanized specimens. The following measurements and their abbreviations are cited in the text; all were taken with electronic digital callipers (0.05 mm accuracy, rounded to the nearest 0.1 mm) as described by Cisneros-Heredia & McDiarmid (2006, 2007): Snout-vent length (SVL), head width (HW), head length (HL), horizontal eye diameter (ED), inter-orbital distance (IOD), eye-nostril distance (EN), internarial distance (IN), width of disc of third finger (3DW), tibia length (TL), and foot length (FL). The following abbreviations are used along the text: Ce. = Centrolene, Co. = Cochranella, H. = Hyalinobatrachium, and N. = Nymphargus. The three Glassfrog species from southeastern Brazil and northern Argentina were excluded from Hyalinobatrachium by Cisneros-Heredia & McDiarmid (2007) and left as incertae sedis. They are listed here as “Hyalinobatrachium” eurygnathum (Lutz, 1925), “Hyalinobatrachium” parvulum (Boulenger, 1895), and “Hyalinobatrachium” uranoscopum (Müller, 1924) to denote that they are not formally attached to any genus within Centroleniidae. Institutional abbreviations used are as follows: DHMECN — División de Herpetología, Sección Vertebrados, Museo Ecuatoriano de Ciencias Naturales, Quito; DFCH-USFQ — Universidad San Francisco de Quito, Quito. Classification of vegetation formations in Ecuador follows Sierra (1999) as modified by Cisneros-Heredia (2006; 2007).

RESULTS

Expeditions to three localities in the Province of Esmeraldas, Ecuador, found one specimen of Cochranella mache each: DHMECN 2611, an adult male collected at night while perched on a herbaceous plant about 1.6 m above a small stream at Monte Saino, Punta Galeras region (00°42’N, 80°01’W, 100 m elevation), on 21 October 2004; DFCH-USFQ LQ23, an adult male found at night perched on a low broadleaf shrub about 1 m above a small stream in old secondary forest about 3 km NW from the town of Quininde (00°21’N, 79°29’W, about 150 m elevation), on 23 March 2005; and, DHMECN 3560, an adult female encountered at night perched on broadleaf herbaceous vegetation (0.87 m above forest floor) about 2.30 m from the edge of a small stream (depth 0.11 m; width 0.89 m) in old secondary forest at the Reserva Biológica Canandé (00°26’N, 79°08’W; c. 270 m elevation), on 24 June 2005. The specimen (DHMECN 3560) collected at Canandé is the first known female of the species. It had unpigmented eggs and was collected at the end of the local dry season. No reproductive activity (calls, territorial males, or females with eggs) was observed for any other centrolenid at the site at that time. When found, the female was using its hind leg to kick an approaching cockroach. Cochranella mache was sympatric with Centrolene prosoblepon (Boettger, 1892), Ce. ilex (Savage, 1967), Co. albo-maculata (Taylor, 1949), and an undescribed species of Cochranella at Canandé; with Ce. prosoblepon, Co. pulverata (Peters, 1873), and Hyalinobatrachium fleischmanni (Boettger, 1893) at Monte Saino; and with Ce. prosoblepon, Ce. litorale Ruiz-Carranza & Lynch, 1996, Co. albornaculata, and H. fleischmanni at the surroundings of Quininde. At its type-locality, Bilwa, Co. mache was sympatric with Ce. prosoblepon, Co. albornaculata, and H. fleischmanni.
The original description of *Cochranella mache* (based solely on males, Guayasamín & Bonaccorsó 2004) is adequate, thus we will not repeat general details about the species' morphology. Instead, we provide information on characteristics of the first female specimen known, additional variation observed, and morphometric and chromatic accounts. The adult female is similar to males in most characters of their general morphology. The main differences include (male characters in parentheses): (1) dorsal skin shagreen and with warts but without spicules (dorsal skin shagreen, usually with numerous minute spicules and warts with protruding spicules); (2) ventrolateral edges of fingers IV, forearms, elbows, toe V, tarsi, and heels with low dermal folds with flat, white [= enameled] tubercles, but sometimes becoming so inconspicuous that just the tubercles are apparent (dermal folds present, conspicuous, with large white tubercles on ventrolateral edges of finger IV, forearms, elbows, toe V, tarsi, and heels); (3) cloacal opening bordered laterally by low, fleshy, tuberculat-ed horizontal flaps but not n-shaped; flat, large, fleshy cloacal enameled tubercles located posterior to cloacal slit and towards the vent (cloacal opening bordered laterally by fleshy tuberculat-ed n-shaped fold; cloacal tubercles small, fleshy, located immediately posterior to cloacal slit); and (4) white coloration restricted to the points of finger I and II, points of toes I and II, but also on the margins of webbing between fingers and toes (entire fingers I and II and toes I and II white, and no white on webbing). Sexual

Table 1: Variation of measurements (in mm) of one female and two male specimens of *Cochranella mache* Guayasamín & Bonaccorsó, 2004. For abbreviations see ‘Materials and Methods’.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>DHMECN 3560 Female / Weibchen</th>
<th>DHMECN 2611 Male / Männchen</th>
<th>DFCH-USFQ LQ23 Male / Männchen</th>
</tr>
</thead>
<tbody>
<tr>
<td>SVL</td>
<td>28.0</td>
<td>22.0</td>
<td>23.5</td>
</tr>
<tr>
<td>HW</td>
<td>8.4</td>
<td>7.5</td>
<td>7.6</td>
</tr>
<tr>
<td>HL</td>
<td>8.4</td>
<td>7.6</td>
<td>7.7</td>
</tr>
<tr>
<td>ED</td>
<td>2.7</td>
<td>2.7</td>
<td>2.6</td>
</tr>
<tr>
<td>IOD</td>
<td>3.8</td>
<td>3.4</td>
<td>3.5</td>
</tr>
<tr>
<td>EN</td>
<td>2.7</td>
<td>2.1</td>
<td>2.3</td>
</tr>
<tr>
<td>IN</td>
<td>2.6</td>
<td>1.7</td>
<td>1.6</td>
</tr>
<tr>
<td>3DW</td>
<td>0.9</td>
<td>0.9</td>
<td>0.9</td>
</tr>
<tr>
<td>TL</td>
<td>16.3</td>
<td>13.8</td>
<td>14.1</td>
</tr>
<tr>
<td>FL</td>
<td>13.6</td>
<td>11.2</td>
<td>11.6</td>
</tr>
</tbody>
</table>

Table 2: Variation of proportions of one adult female and two male specimens of *Cochranella mache* Guayasamín & Bonaccorsó, 2004. For abbreviations see ‘Materials and Methods’.

<table>
<thead>
<tr>
<th>Proportion</th>
<th>DHMECN 3560 Female / Weibchen</th>
<th>DHMECN 2611 Male / Männchen</th>
<th>DFCH-USFQ LQ23 Male / Männchen</th>
</tr>
</thead>
<tbody>
<tr>
<td>HW/HL</td>
<td>1.00</td>
<td>0.99</td>
<td>0.99</td>
</tr>
<tr>
<td>HW/SVL</td>
<td>0.30</td>
<td>0.34</td>
<td>0.32</td>
</tr>
<tr>
<td>HL/SVL</td>
<td>0.30</td>
<td>0.34</td>
<td>0.33</td>
</tr>
<tr>
<td>EN/HL</td>
<td>0.32</td>
<td>0.28</td>
<td>0.30</td>
</tr>
<tr>
<td>ED/HL</td>
<td>0.32</td>
<td>0.35</td>
<td>0.34</td>
</tr>
<tr>
<td>IOD/ED</td>
<td>1.39</td>
<td>1.28</td>
<td>1.35</td>
</tr>
<tr>
<td>EN/ED</td>
<td>1.00</td>
<td>0.79</td>
<td>0.88</td>
</tr>
<tr>
<td>EN/IOD</td>
<td>0.72</td>
<td>0.62</td>
<td>0.66</td>
</tr>
<tr>
<td>3DW/ED</td>
<td>0.31</td>
<td>0.32</td>
<td>0.35</td>
</tr>
<tr>
<td>TL/SVL</td>
<td>0.58</td>
<td>0.63</td>
<td>0.60</td>
</tr>
<tr>
<td>FL/SVL</td>
<td>0.48</td>
<td>0.51</td>
<td>0.49</td>
</tr>
</tbody>
</table>
Fig. 1: Alive female *Cochranella mache* GUAYASAMIN & BONACORSO, 2004 (DHMECN 3560) showing a blue dorsum with a yellow patch on the head and abundant small orange spots. Photographed by Jesse Delia.

Abb. 1: Im Leben zeigt das Weibchen von *Cochranella mache* GUAYASAMIN & BONACORSO, 2004 (DHMECN 3560) einen blauen Rücken mit einem gelben Fleck auf dem Kopf und zahlreiche kleine orangefarbene Flecken. Photo: Jesse Delia.
Dimorphism in size is evident, being that the female is larger than known males. No other relevant morphometric differences in gross measurements or proportions were found among males and females but the small sample size prevents conclusive assessment (Tables 1 and 2).

A low supratympanic fold, obscuring the posterodorsal portion of the tympanic annulus, was reported in the type series. Intraspecific variation on this character is noted as some specimens lacked the supratympanic fold in life, and the entire perimeters of their tympanic annuli were apparent. There is variation on the relationship between the first and second fingers, both can be of approximately the same length (as reported in the original description) or finger I slightly longer than finger II. All examined specimens of Co. mache have iridophores covering the parietal peritoneum, pericardium, and the peritonea covering the esophagus, stomach, intestines, and gonads, as reported originally. However, two specimens (DHMECN 3560 and DFCH-USFQ LQ23) show iridophores forming isolated small patches on the ventral and lateral surfaces of the hepatic peritoneum (not covering the entire liver as in H. fleischmanni). The type-series and specimen DHMECN 2611 lack iridophores over the hepatic peritoneum (pers. obs., GUAYASAMIN & BONACCORSO 2004). In addition, two specimens have the renal capsules covered by iridophores (DHMECN 2611 and DHMECN 3560).

Continuous observations on specimen DHMECN 3560 while alive revealed that Cochranella mache performs profound chromatic changes. Originally, Co. mache was described as having a green dorsum (better described as bluish-green...
by analyzing the photos of the holotype available at AmphibiaWeb) with small yellow spots, upper lip with thin white margin, throat and ventral surfaces of limbs bluish-green, iris white with fine black reticulation, and a narrow golden ring around pupil. When collected, DHMECN 3560 showed a similar coloration to the original description. A particular feature became apparent, the presence of a large dull yellow-colored patch on the top of the head. This patch is also observed on the photograph of the holotype of Cochranella mache, but it was not mentioned in the original description. After been taken to the laboratory for analysis, the background coloration of the individual turned completely light blue (slightly lavender towards the sides), the patch on the head bright yellow, the iris light lavender with dark lavender reticulations and the pupillary ring became less evident by turning white with a blue hue (Figure 1). The dorsal spots varied from ochre yellow to bright orange, always becoming brighter towards the head.

DISCUSSION

Cochranella mache is a nocturnal species associated with small streams across primary and old-secondary forests in the Cordillera Mache-Chindul, endemic to the Seasonal Evergreen Forest of the Ecuadorian Region. Although just one female specimen is currently available, some preliminary tendencies about the sexual dimorphism in the species are observed. Cochranella mache shows the same SVL dimorphism present in most glassfrogs, with females larger than males (the only known exception in the family is Centrolene geckoideum Jiménez de la Espada, 1872). The presence of spicules on the skin of breeding males, but absent in females, is also a widespread condition in centrolenids, and many other frogs (e.g., Osteocephalus). Variation in the expression of dermal folds and cloacal ornaments has been reported in several species of centrolenids, not necessarily related to sexual dimorphism (e.g., Heyer 1978, 1985). It is worthwhile to mention that the intraspecific variation herein reported for Co. mache is parallel to the differences used to distinguish Cochranella phryxa Aguayo & Harvey, 2006 from Cochranella resplendens (Lynch & Duellman, 1973) by Aguayo & Harvey (2006), suggesting that in fact, Co. phryxa could be a synonym of Co. resplendens (Cisneros-Heredia & McDiarmid 2007).

The presence of iridophores on the hepatic peritoneum was a condition conceived by Ruiz-Carranza & Lynch (1991) as restricted only to the genus Hyalinobatrachium. However, further research has showed that it is a widespread condition in most genera currently recognized in the family Centrolenidae (absent in Nymphargus), and even across Hylid genera (Noonan & Harvey 2000; Duellman & Señaris 2003; Cisneros-Heredia & McDiarmid 2006). Apart from species of the genus Hyalinobatrachium (sensu Cisneros-Heredia & McDiarmid 2007), twelve centrolenid species have iridophores on the hepatic peritoneum: Centrolene gorzelai (Ayarzagüena, 1992), Ce. lema Duellman & Señaris, 2003, Ce. mariaeleges Cisneros-Heredia & McDiarmid, 2006, Ce. papillallicium Noonan & Harvey, 2000, Cochranella antithenesi (Goin, 1963), Co. amelie Cisneros-Heredia & Meza-Ramos, 2007, Co. castroviejoi Ayarzagüena & Señaris, 1997, Co. helenae (Ayarzagüena, 1992), Co. pulverata (Peters, 1873), “Hyalinobatrachium” parvulum, “Hyalinobatrachium” eurygnathum, “Hyalinobatrachium” uranoscopum (Ruiz-Carranza & Lynch 1991; Noonan & Harvey 2000; Duellman & Señaris 2003; Señaris & Ayarzagüena 2005; Cisneros-Heredia & McDiarmid 2006, 2007; Cisneros-Heredia & Meza-Ramos 2007). However, all these taxa have iridophores covering the entire surface of the hepatic peritoneum; while the two specimens of Co. mache herein reported just have isolated patches — a condition previously reported only in Co. phryxa (Aguayo & Harvey 2006). The presence of iridophores on the hepatic peritoneum of Co. mache is subjected to intraspecific variation, and apparently, not equivalent to the
Cochranella mache was originally described as having a green dorsal coloration in life (Guayasamin & Bonaccorso 2004); a feature shared with most glassfrogs, which usually show different shades of green in their background coloration (Cisneros-Heredia & McDiarmid 2007). Although a few centrolenid species have been described as having different colours, usually shades of brown, e.g., Nymphargus anomalous (Lynch & Duellman, 1973) and N. rosada (Ruiz-Carranza & Lynch, 1997), and Cochranella granulosa (Taylor, 1949) shows a bluish-green background dorsal color; a deep blue glassfrog has not been reported before (Cisneros-Heredia & McDiarmid 2007). While searching images of centrolenids on the internet, we found a photograph of Cochranella euknemos (Savage & Starrett, 1967) showing a completely blue dorsal background (Gardner 2007). Cochranella mache has been hypothesized to be closely related to Cochranella granulosa (member of the former “Co. granulosa species-group”; Ruiz-Carranza & Lynch 1991; Guayasamin & Bonaccorso 2004; Cisneros-Heredia & McDiarmid 2007). Although that former group is not monophyletic (as suggested by the different reproductive patterns of some of its members, Cisneros-Heredia & McDiarmid 2007), we agree that Co. mache is related to Co. granulosa and Co. euknemos, and probably the sister-species of the last one. All three species share an apparently similar chromatophore organization that gives them a bluish-green to blue dorsal coloration (Kubicki 2007, this work). Further, Co. mache and Co. euknemos show three unique characters (synapomorphies) that support our conclusion: the presence of a yellow-colored patch on the top of the head, the presence of iridophores on the fingers and toes, usually in the points (see photos of Co. euknemos presented by Kubicki 2007), and the capacity of changing their dorsal background coloration from bluish-green to deep blue.

The original description of Co. mache compared it only with other members of the former “Co. granulosa species group”. During the herpetological surveys where Co. mache was collected, some specimens of Co. pulverata were also found (see Bustamante et al. 2007). Both species may be confused, particularly in preservative, thus we provide some diagnostic characters to differentiate between them. Cochranella pulverata differs from Co. mache by having the parietal peritoneum entirely clear (without iridophores), while the hepatic peritoneum is completely white (covered by iridophores); the dorsal spots are white in life (never yellow or orange), and more abundant and smaller than those present in Co. mache; the webbing of Co. pulverata between finger II and III is slightly more extended; its enameled cloacal ornamentation does not show a n-shaped or horizontal flap, and the cloacal folds are low and not fleshy; males of Co. pulverata have low dermal folds on the ventrolateral edges of fingers IV, forearms, elbows, toe V, tarsi, and heels, less pronounced than those in the males of Co. mache. The dorsal coloration of Co. pulverata is green in life (without any bluish tint and without a yellow head patch) and turns light lavender-cream after a short time in preservative. While Co. pulverata is externally similar to some species currently considered as related to Co. granulosa (especially by its snout that is gradually inclined in lateral aspect), it clearly differs by the iridophores conditions on its peritoneum. Cochranella pulveratum was placed together with Co. antisthenesi in the former “H. pulveratum species-group” by Ruiz-Carranza & Lynch (1991), but both species do not seem to be closely related to each other or to Hyalinobatrachium (Cisneros-Heredia & McDiarmid 2006; 2007).

In order to provide taxonomists with data useful in characterizing Co. mache, a numbered diagnosis is provided including new information reported in this paper: (1) vomerine teeth present; (2) snout subacuminate in dorsal view, and gradually sloping in lateral view (Figure 2); (3) tympanic annulus evident, oriented dorsolaterally with slight dorsal inclination; and supratympanic fold weak or absent; (4) dorsal skin shagreen with warts — usually corresponding to light spots; males (in reproductive condition) with numerous minute spinules and protruding spicules on the warts, females without spinules or spicules; (5) ventral skin granular; several round, flat or large enam-
eled warts tubercles on ventral surfaces of thighs below vent, and around the cloacal opening; and fleshy, tuberculated, enameled cloacal fold present, large and n-shaped fold in males but low and horizontal flaps in females; (6) anterior 1/3 of parietal peritoneum covered by iridophores (white); iridophores over pericardium and visceral peritoneum (digestive tract, and gonads); hepatic peritoneum clear or with small, isolated patches of iridophores; and renal capsules covered by iridophores in some specimens; (7) liver tetralobed; (8) humeral spine absent in adult males; (9) webbing on hand, absent between fingers I and II, I (1–1)<(3–3) III (2–2)<(1–1) IV (Figure 2); (10) webbing on foot, I (1–1)<(2–2) II (1–1)<2 III (1–1)<2 IV (2–2)<(1–1) V (Figure 2); (11) ventrolateral edges of fingers IV, forearms, elbows, toe V, tarsi, and heels with dermal enameled folds and tubercles; conspicuous folds and large tubercles in males (Figure 2); and low or inconspicuous folds and low tubercles in females; (12) large nuptial pad Type I, concealed prepollex; (13) first finger slightly longer or about the same length of second finger; (14) eye diameter larger than width of disc on finger III; (15) color in life, dark olive-green to blue-lavender or light blue dorsum with numerous small yellow to orange spots, large dull to bright yellow patch on top of head; fingers I and II and toes I and II entirely (males) or partially (females) white; and webbing on hands and feet white in females; (16) color in preservative, dorsal surfaces pale lavender with small white or cream spots; tubercles on dermal folds of limbs, fingers, and toes cream-white; inner fingers and toes white or unpigmented (Figure 2); (17) iris white to pale lavender with fine black to dark lavender reticulations; and a narrow golden ring apparent in some specimens; (18) melanophores present along the entire dorsal surfaces of fingers and toes except for areas covered by iridophores on inner fingers and toes; (19) males called from upper side of leaves over streams; (20, 21, 22, 23) advertisement call, fighting behavior, egg clutches, and tadpoles unknown; and (24) snout-vent length in adult males 22.0–24.0 mm (n = 5); in adult female 28.00 mm (n = 1).

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REFERENCES


Presentamos nueva información sobre la historia natural y variación intraespecífica de Cochranella mache Guayasamin & Bonaccorsko, 2004. Esta es una especie nocturna que vive asociada a riachuelos pequeños en bosques primarios y secundarios en la Cordillera Mache-Chindul, siendo una especie endémica a los Bosques Siempreverdes Estacionales de la región biogeográfica del Oeste Ecuatoriano. La variación intraespecífica y dimórfica es observada en varios caracteres, incluyendo la textura de la piel dorsal, la expresión de los pliegues dérmicos, la ornamentación cloacal, la expresión del pliegue supratimpánico y la extensión de los iridóforos en el peritoneo hepático. Cambios cromáticos dramáticos en vida son reportados, mostrando un patrón único en Centrolenidae, su patrón dorsal cambia de verde azulado con un parche amarillo pálido en la cabeza y abundantes puntos amarillo, hacia un dorso lavanda/celeste con un parche amarillo brillante en la cabeza y abundantes puntos naranja. Con el objetivo de proveer a futuros investigadores con datos útiles para caracterizar la especie, presentamos una diagnosis numerada para Co. mache, incluyendo toda la nueva información.