



***Centrolene daidaleum* (Ruiz-Carranza & Lynch, 1991) (Anura, Centrolenidae): A glassfrog with primitive and derived combat behavior**

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Glassfrogs (family Centrolenidae) constitute a diverse Neotropical group of epiphyllous and arboreal anurans (Señaris & Ayarzagüena 2005; Guayasamin *et al.* 2009). They are commonly encountered on stream-side vegetation and many species may show high densities during their reproductive season, with numerous territorial males calling for mates in relative small areas (Señaris & Ayarzagüena 2005; Kubicki 2007; Delia *et al.* 2010). Territoriality of males in several glassfrog species occasionally implies combat behaviors. Combat behavior has been poorly documented in glassfrogs, mainly reported from anecdotal observations in just 11 species (McDiarmid & Adler 1974; Duellman & Savitzky 1976; Greer & Wells 1980; Jacobson 1985; Restrepo-Toro 1996; Bolívar *et al.* 1999; Savage 2002; Guayasamin & Barrio-Amorós 2005; Kubicki 2007; Delia *et al.* 2010).

Combat behavior between males was first proposed as an important character to resolve the intergeneric relationships of glassfrogs (*sensu* Ruiz-Carranza and Lynch 1991a) by Bolívar *et al.* (1999). Two states were described for this behavioral character: a primitive state, consisting of males fighting in an amplexus-like position on leaf surfaces, which was predicted for all species of *Hyalinobatrachium* (*sensu* Ruiz-Carranza & Lynch 1991a); and a derived state, in which males grapple venter-to-venter while dangling upside down by their feet holding vegetation, proposed as synapomorphy for *Centrolene* and *Cochranella* (*sensu* Ruiz-Carranza & Lynch 1991a).

In a recent major revision of Centrolenidae (Guayasamin *et al.* 2009), combat behavior was also recognized as a taxonomic character, but to discriminate groups at subfamilial level. Primitive combat behavior (wrestling on leaves) was hypothesized as restricted to Hyalinobatrachinae, which unlike the phylogeny used by Bolívar *et al.* (1999) to examine the distribution of combat character states, includes the genus *Celsiella*, composed by two species previously included in *Cochranella* (*sensu* Ruiz-Carranza & Lynch 1991a). On the other hand, derived combat behavior (grappling venter-to-venter while dangling upside down) was considered as a primary homology of Centroleninae (Guayasamin *et al.* 2009).

In this work we describe the first observation of combat in *Centrolene daidaleum*, a species assigned to the subfamily Centroleninae, and which includes both primitive and derived fighting behavior.

Centrolene daidaleum is distributed through the western slope of the Cordillera Oriental in Colombia and the eastern slope of the Sierra de Perijá in Venezuela (Ruiz-Carranza & Lynch 1991b; Daza-R & Barrientos 2005; Rada *et al.* 2007; Rada & Guayasamin 2008; Rojas-Runjaic *et al.* 2010).

Combat behavior of *Centrolene daidaleum* was observed on 19 March 2009, along a fast-flowing stream affluent of the Río Negro, near indigenous community of Manastara (10°02'52"N, 72°48'43"W; 1130 m asl) in the Sierra de Perijá, Estado Zulia, Venezuela. The observation started at 20:04 h, during an overcast night, after a calm rain. The contenders were discovered after combat had begun, and were detected by the encounter calls (McDiarmid & Adler, 1974) emitted by both individuals. The calls emitted during combat consisted of a low pitched “preep”, audibly different from their typical advertisement call, which is a shorter and higher-pitched single or double note “peep” (Cardozo, 2010).

The pair was located on the upper surface of a leaf, about 1.2 m above the stream. They were fighting on the center of the leaf in an amplexus-like position (Fig. 1a). Both frogs repeatedly emitted encounter calls and maintained their vocal sacs partially inflated (Fig. 1l). The male in the lower position (A) repeatedly pushed upward his opponent (B) with his head or hind legs, breaking the “amplexus” like hold by the opposing male (B) several times (Fig. 1b). Simultaneously B pulled its opponent upward and sideways while hugged from axillae, throwing A to the edge of the leaf several times (Fig. 1c). After each jerk from B, A reacted by anchoring himself with his legs extended along the surface of the leaf, then moved quickly to the center of the leaf, carrying B on its back. After several minutes, A broke free from the axillary hold by B, reared its body upward on its feet and grabbed B in an upright venter-to-venter position.