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Combat behavior in *Centrolene buckleyi* and other centrolenid frogs

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Observations of fighting behavior in *Centrolene buckleyi* revealed that males dangled by their feet and grappled venter-to-venter. One of the males repeatedly uttered a soft, short squeak, inflating the vocal sac and prying off the other combatant in the process. Sonagrams of this aggressive call and the advertisement call reveal markedly different structures. Both frogs were visibly injured, presumably in combat. Of the few species coded for combat behavior ($n = 7$), those of the genera *Centrolene* and *Cochranella* exhibit the derived state of dangling by the feet and grappling venter-to-venter, whereas species of *Hyalinobatrachium* have primitive combat composed of one male grasping the other in amplexus. We predict that the derived behavior will be discovered in all *Centrolene* and in all or a large part of *Cochranella* (representing a synapomorphy that unites the two groups), and that no *Hyalinobatrachium* species will exhibit the apomorphic state.

INTRODUCTION

Although the past few decades have seen an unprecedented increase in our knowledge of centrolenid frogs, most workers have concentrated on resolving taxonomic and phylogenetic issues from a strictly morphological perspective. In so doing, they have inadvertently ignored an abundance of characters that could provide invaluable clues as to the relationships of these frogs. The purposes of this paper are to describe the physical combat of *Centrolene buckleyi* (Boulenger, 1882) and to discuss the phylogenetic significance of combat behavior in the family Centrolenidae.

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METHODS

Our observations of *Centrolene buckleyi* combat were made on 2 April 1996, just below El Boquerón, near the border between Departamento del Valle del Cauca and Departamento del Chocó at 2220 m in the Cordillera Occidental of Colombia (GPS coordinates: 4°44′39″N, 76°18′16″W). The site is in relatively intact cloud forest along the road from El Cairo to El Boquerón.

The frogs were found at the side of the road approximately 2.5 m directly above a trickle of run-off water and 6 m from a fast flowing stream along which we heard many advertisement calls of this species. It rained quite heavily throughout most of the day and night, before, during and after these observations.

Calls were recorded using a Sony WM D6C Professional Walkman and a Sony ECM 909 microphone at 15.6°C air temperature. Sonagrams were generated on a Kay 5500 DSP Sona-Graph. Data were also obtained using Computerized Speech Research Environment (CSRE) 4.5 PC-based signal analysis software.

Preserved specimens are kept in the Universidad del Valle Colección de Anfibios y Reptiles (UVC).

RESULTS

Our observations began at 22.05 h. Frog A (UVC 12729; SVL 28.7 mm) was hanging from a horizontal twig by its feet and was grasping frog B (UVC 12730; SVL 27.9 mm) with its hands at the base of B's arms. B was grasping A in the same way, but was hanging with its feet free. The two frogs were facing the same direction.

B began swinging its body and grasped a leaf with its foot. After several minutes, it swung its body up and wrapped its feet and legs around A's body. At this point the two frogs were oriented venter-to-venter, hanging head down (fig. 1).

A then began to emit a call sporadically, consisting of a single, short, soft squeak lasting 0.14–0.15 s (fig. 2A). The frequencies of this call fall between 4000 and 7100 Hz and are strongly modulated. The emphasized frequency begins at around 4600 Hz and climbs to near 5000 Hz, at which point it jumps to about 7100 Hz and then rather abruptly falls to terminate near 6000 Hz. The first part of the call is notably pulsatile (although the number and pattern of pulses is variable), while the second, higher, part is only weakly so. When A called, the vocal sac expanded, which, in turn, pushed B from A, thereby loosening B's grip. After several minutes of this behavior, at 22.42 h, B fell to a leaf below, at which time it was collected. A climbed up onto the twig from which it had been hanging, and it was also collected. The observed combat lasted 37 min.

Both frogs were visibly wounded, presumably in combat. B, the "loser" of the encounter, had a red, swollen hematoma just dorsal and slightly anterior to the insertion of the right arm; the location of the injury corresponds to the position of A's humeral spine during combat. While A did not show any wounds or marks directly attributable to B's humeral spine, the skin

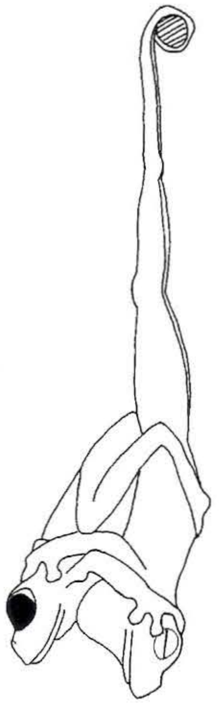

Fig. 1. – Illustration of combat in *Centrolene buckleyi*

on the dorsal surface of the outer edge of the right hand and fingers III and IV was torn. The right hand was observed not to be used when climbing in the plastic collecting bag. Both specimens were sluggish once collected.

DISCUSSION

The above description conforms well with descriptions of combat in *Cochranella griffithsi* Goin, 1961 (DUELLMAN & SAVITZKY, 1976) and *C. ignota* Lynch, 1990 (RESTREPO-TORO, 1996), both of which lack the humeral spine in males (although *C. griffithsi* males exhibit "a large bladelike ventral crest on the humerus"; LYNCH & RUIZ-CARRANZA, 1997: 529, fig. 3). Similar fighting has also been observed in *Centrolene prosoblepon* (Boettger, 1892) by JACOBSON (1985) and *C. acanthidiocephalum* (Ruiz-Carranza & Lynch, 1989) by Pedro M. RUIZ-CARRANZA (personal communication), two species which exhibit a humeral spine in males.

There are two differences between previous observations and ours. First, previous reports have not mentioned any evidence of physical damage inflicted by the humeral spine (although JACOBSON observed seven combat encounters). It is common to find scars on the head and body of males of *Centrolene geckoideum* Jiménez de la Espada, 1872 (personal

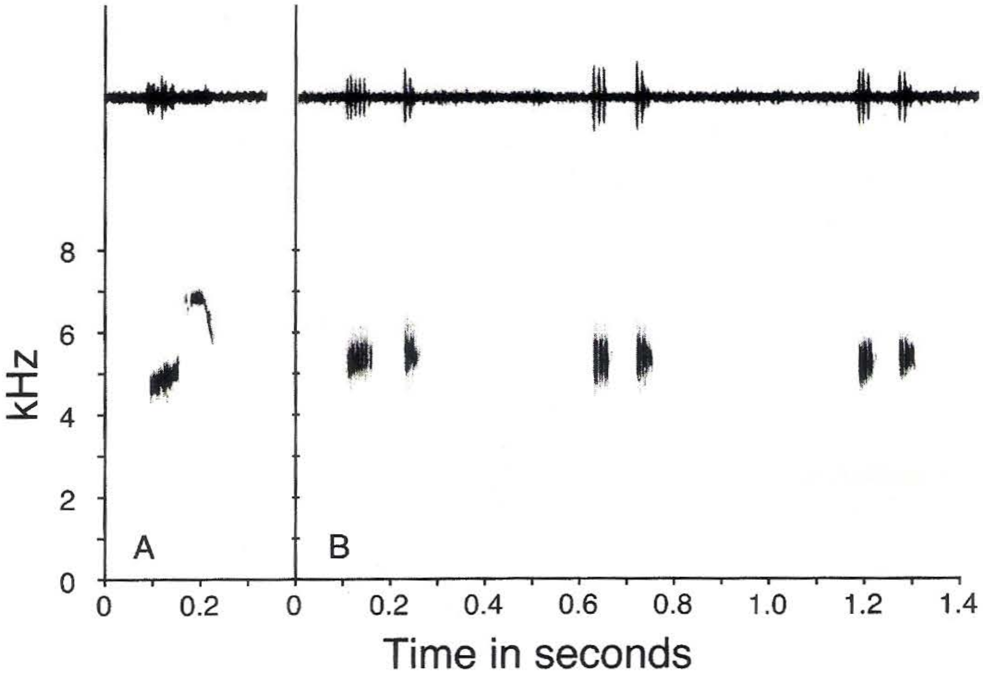

Fig. 2. – Audiospectrograms (graphed with wide-band 300-Hz filter) and waveforms of *Centrolene buckleyi* vocalizations, both recorded at 15.6°C air temperature, produced from tape copy on AMNH herpetology reel 276. (A) Combat call of UVC 12729. (B) Advertisement call of UVC 12589; *C. buckleyi* was observed to call sporadically, i.e., couplets are not usually emitted in series.

observation), presumably inflicted in combat by the extremely large and sharp spines of this species (as opposed to the blunt spine of *C. buckleyi*; see Ruiz-Carranza & Lynch, 1991, and Rueda-Almonacid, 1994, for spine shape and size in *C. buckleyi* and *C. geckoideum*, respectively), but to date combat has not been observed to confirm this suspicion. Our evidence of physical damage inflicted by the humeral spine is circumstantial (i.e., we did not examine the individual immediately prior to combat, so we cannot confirm the origin of the hematoma) but is more convincing than any previously reported.

The second difference is the use of a call during combat. Our interpretation of this event as non-accidental is based on the fact that we observed frog A to produce over 25 such calls (including 14 in recordings TG 9604 and 9605), all with the same effect. Inasmuch as the call – or, more precisely, the inflation of the vocal sac – appeared to be used to physically loosen the opponent's grip during combat, we suspect that the acoustic qualities of the call are unimportant. Despite this conjecture, the call varies remarkably little; all of the calls recorded exhibit essentially the same amplitude and frequency modulation as that shown in fig. 2A, i.e., it is not simply a random emission of sound made while inflating the vocal sac. As seen in fig. 2, this call differs markedly from the advertisement call (fig. 2B), which is a high-pitched,

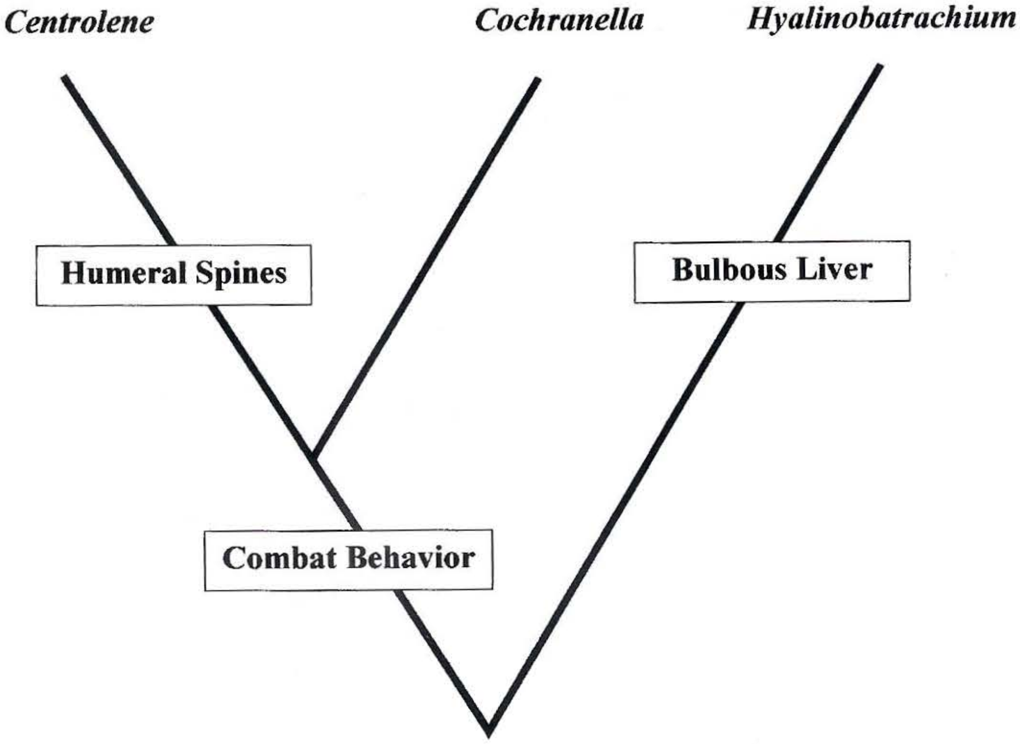

Fig. 3. – Conjectured phylogeny of centrolenid genera based exclusively on unique synapomorphies, i.e., character states that do not occur in any other anuran.

pulsed croak of 0.12–0.15 s duration consisting of two notes; the first note contains between three and six well defined pulses, while the second note contains three. The two notes are separated by 0.05–0.06 s intervals. The emphasized frequency lies at approximately 5200 Hz. The aggressive call also differs acoustically from the short, sporadic bursts of random noise that compose the encounter call of *Centrolene buckleyi* (fide John D. LYNCH, personal communication). Although B is an adult with vocal slits, it was not observed to call during the event.

The physical combat of frogs of the genus *Hyalinobatrachium* differs from that of *Centrolene* and *Cochranella*. MCDIARMID & ADLER (1974) described the combat behavior of *H. fleischmanni* (Boettger, 1893) (as *Centrolenella viridissima* Taylor, 1942) and *H. valerioi* (Dunn, 1931), in which one of the males grasps the other in amplexus; their description of *H. fleischmanni* combat was corroborated by GREER & WELLS (1980) and JACOBSON (1985). Strict outgroup comparison (sensu LYNCH, 1997: 355, footnote 2) reveals that this is the primitive behavior, while combat in which males dangle by their feet grappling venter-to-venter is derived.

Although the data set is exceedingly small (data are available for only 6.1 % of the family), it is sufficient to allow us to make a number of predictions based on a cladistic interpretation of known character distribution and published phylogenetic hypotheses (primarily RUIZ-CARRANZA & LYNCH, 1991). First, we predict that the derived combat will be found in all 33 species of *Centrolene* for which combat remains to be observed. Similarly, we predict that none of the 24 uncoded species of *Hyalinobatrachium* will exhibit this derived state (i.e., they will exhibit either the plesiomorphic state or some other, unknown type of combat). Convincing evidence of monophyly has not been put forth for the more than 50 species (or any sizeable portion thereof) placed in *Cochranella*. However, the expression of the derived type of combat in two small but seemingly quite distantly related monophyletic groups of *Cochranella* – viz., the *ocellata* group sensu stricto (i.e., sensu LYNCH, 1990) and the *griffithsi* group (sensu LYNCH & RUIZ-CARRANZA, 1997: 529; named by RUIZ-CARRANZA & LYNCH, 1995: 3) – is suggestive of a widespread distribution of this state throughout *Cochranella*. Consequently, we postulate (fig. 3) that the derived combat behavior constitutes a synapomorphy for *Centrolene* + (at least some part of) *Cochranella*, and therefore resolves the polytomy reported by RUIZ-CARRANZA & LYNCH (1991). Data on the use of an aggressive call in combat are too limited ($n = 1$ species) to be phylogenetically informative at this time.

RESUMEN

En nuestras observaciones del combate físico de *Centrolene buckleyi*, los machos se colgaron de los pies y pelearon vientre-a-vientre. Un macho emitió repetidamente un chillido débil y corto, y así inflaba la bolsa vocal y empujaba al otro combatiente en el proceso. Los sonogramas de este canto agresivo y el canto de advertencia demuestran estructuras marcadamente diferentes. Cuando las colectamos, ambas ranas estaban visiblemente heridas, presumiblemente durante el combate. De las pocas especies codificadas por el comportamiento de combate ($n = 7$), *Centrolene* y *Cochranella* exhiben el estado derivado de colgarse de los pies y pelear vientre-a-vientre, mientras que *Hyalinobatrachium* presentan el combate primitivo en el cual un macho agarra al otro en amplexus. Predecimos que se descubrirá el comportamiento derivado en todas las especies de *Centrolene* y una gran parte de *Cochranella* (y por ende representa una sinapomorfia para estos dos grupos), y que ninguna especie de *Hyalinobatrachium* presentará el estado apomórfico.

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LITERATURE CITED

DUELLMAN, W. E. & SAVITZKY, A. H., 1976. – Aggressive behavior in a centrolenid frog, with comments on territoriality in anurans. *Herpetologica*, **32**: 401-404.

GREER, B. J. & WELLS, K. D., 1980. – Territorial and reproductive behavior of the tropical American frog *Centrolenella fleischmanni*. *Herpetologica*, **36**: 318-326.

JACOBSON, S. K., 1985. – Reproductive behavior and male mating success in two species of glass frogs (Centrolenidae). *Herpetologica*, **41**: 396-404.

LYNCH, J. D., 1990. – A new ocellated frog (Centrolenidae) from western Colombia. *Proc. biol. Soc. Washington*, **103**: 35-38.

----- 1997. – Intrageneric relationships of mainland *Eleutherodactylus*. II. A review of the *Eleutherodactylus sulcatus* group. *Rev. Acad. colomb. Cienc.*, **21**: 353-372.

LYNCH, J. D. & RUIZ-CARRANZA, P. M., 1997. – A remarkable new centrolenid frog from Colombia with a review of nuptial excrescences in the family. *Herpetologica*, **52**: 525-535.

MCDIARMID, R. W. & ADLER, K., 1974. – Notes on territorial and vocal behavior of Neotropical frogs of the genus *Centrolenella*. *Herpetologica*, **30**: 75-78.

RESTREPO-TORO, J. H., 1996. – *Ecología conductual de una rana arbórea Neotropical*.Tesis de Magister, Universidad del Valle, Cali.

RUEDA-ALMONACID, J. V., 1994. – Estudio anatómico y relaciones sistemáticas de *Centrolene geckoideum* (Salientia: Anura: Centrolenidae). *Trianea*, **5**: 133-187.

RUIZ-CARRANZA, P. M. & LYNCH, J. D., 1991. – Ranas Centrolenidae de Colombia. I. Propuesta de una nueva clasificación genérica. *Lozania*, **57**: 1-32.

----- 1995. – Ranas Centrolenidae. V. Cuatro nuevas especies de *Cochranella* de la Cordillera Central. *Lozania*, **62**: 1-23.

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