



Tadpole buccal secretory glands as new support for a Neotropical clade of frogs

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Abstract

Phylogenetic hypotheses of species of *Leptodactylus* have been proposed but relationships often consider few species and high-level groups are supported by few, homoplasious morphological characters. Similarities between the reproductive biology of species of the *L. marmoratus* (formerly *Adenomera*) and those of the *L. fuscus* group may represent homoplasies or, as previously suggested, shared derived features pointing to their closer relationship. We determined the presence of buccal foaming glands in tadpoles of three species of *Leptodactylus* (*L. furnarius*, *L. labyrinthicus* and a member of the *L. marmoratus* group) by histological preparations. The presence of these glands and other seven characters were mapped onto two alternative topologies in order to understand the relationships among *Leptodactylus* species groups and the evolution of their reproductive features. Two sets of foaming glands were found in all species studied: 1) rows of secretory ridges and 2) secretory pits. Mapping the nine characters on the currently recognized phylogeny (emphasizing closer relationship among *L. latrans*, *L. fuscus* and *L. labyrinthicus*) resulted in sixteen steps (CI = 56; RI = 22); in the alternative hypothesis (closer relationship between *L. marmoratus* group and *Leptodactylus* of the *L. fuscus* groups) it resulted in eleven steps (CI = 82; RI = 78). Our evidences support that species in the *L. marmoratus* group are not the sister group to the remainder of *Leptodactylus*, but probably a subset of the *L. fuscus* group.

Key words: Anura, *Leptodactylus*, systematics, phylogeny, Species group, Foaming behavior, Foam nests. *Lithodytes*

Introduction

As presently defined, the genus *Leptodactylus* is a Neotropical taxon with about 90 recognized species (Frost 2011). Phylogenetic hypotheses of component species have been proposed, but were based on molecular data for only a few species and higher level taxa (i.e. species groups) often are supported by few, homoplasious morphological characters (De Sá *et al.* 2005; Ponssa 2008; Ponssa *et al.* 2010). Such a weak phylogenetic support has generated debates on the interpretation of the evolution of their intriguing reproductive features (Kokubum & Giaretta 2005; De Sá *et al.* 2005; Ponssa & Barrionuevo 2008).

All known leptodactylids lay eggs amidst a foam nest, which results from the male vigorous beating the female cloacal fluids during oviposition (Heyer 1977; Duellman & Trueb 1986). This behavior also are widespread among the Neotropical Leiuperidae (Hödl 1986), which formerly was placed in Leptodactylidae (Lynch 1971; Heyer 1975; Roelants *et al.* 2007). It has been demonstrated that the tadpoles of some species of the *Leptodactylus fuscus* (Schneider) (*sensu* Heyer 1978), *L. pentadactylus* (Laurenti) (*sensu* Heyer 2005) and *L. marmoratus* (Steindachner) (*sensu* Heyer 1974) (formerly *Adenomera* Steindachner, Frost *et al.* 2006) species groups replace the parental foam in the nest by releasing bubbles (i.e. air trapped in mucous) through their mouths (Downie 1984, 1989; Caldwell & Lopes 1989; Giaretta & Kokubum 2004; Kokubum & Giaretta 2005; Kokubum & Sousa 2008; Ponssa & Barrionuevo 2008; Oliveira-Filho & Giaretta 2008; Silva & Giaretta 2009). Downie (1989) showed that in *L. fuscus* the larval structures involved in mucous/foam production are highly active epithelial glands located in the posterior part of the buccal roof and in the corners of the ventral velum (Wassersug 1976). In some other frogs these glands are mostly undifferentiated and related to food trapping (Downie 1989). Kokubum & Giaretta (2005) and Silva & Giaretta (2009) called attention to the fact that tadpole foam production is not universal among *Lepto-*