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Article



Direct development in some Australopapuan microhylid frogs of the genera Austrochaperina, Cophixalus and Oreophryne (Anura: Microhylidae) from northern Australia and Papua New Guinea

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Abstract

Embryonic development in fifteen Australopapuan microhylid frogs of the genera Austrochaperina, Cophixalus and Oreophryne is described. These frogs have direct development during which the embryo develops to a minute froglet within the jelly capsule. Development of the operculum, presence of external gills, tail structure, gut development and timing of forelimb emergence are described and compared with the direct-developing eleutherodactylid *Eleutherodactylus coqui* from Puerto Rico and three Australian myobatrachid genera with direct development (*Arenophryne, Metacrinia* and *Myobatrachus*). We comment on those differences that likely reflect examples of convergent and divergent evolution and heterochrony.

Key words: frog, embryo, *Cophixalus aenigma, C. concinnus, C. cryptotympanum, C. hosmeri, C. neglectus, C. ornatus, C. riparius, C. saxatilis, Austrochaperina adelphe, A. fryi, A. pluvialis, A. robusta, Eleutherodactylus, Oreophryne*

Introduction

Direct development, in which embryos bypass the aquatic larval stage and hatch from the egg as small frogs (Duellman & Trueb 1986; Thibaudeau & Altig 1999; Desnitskiy 2010), is one of the most extreme evolutionary modifications of amphibian life histories. This reproductive strategy has evolved independently at least 10 times in anurans (Duellman & Trueb 1986) resulting in many hundreds of direct-developing species that are mainly found in tropical regions. The anuran family Microhylidae has a predominantly tropical global distribution, and members of the family exhibit a diversity of reproductive strategies (Duellman & Trueb 1986; Thibaudeau & Altig 1999). Direct development has to date only been documented in one currently recognised microhylid subfamily, the Aster-ophryinae (Thibaudeau & Altig 1999; Zweifel, 2000; Frost *et al.* 2006; Frost 2011; Matsui *et al.* 2011).

The microhylid subfamily Asterophryinae reaches its greatest diversity in New Guinea, where it is represented by 23 genera (Frost 2011; including *Gastrophrynoides*: Matsui *et al.* 2011). Of these, some members of the three genera *Cophixalus* Boettger 1892 (at least 30 species), *Austrochaperina* Fry 1912 (23 species) and *Oreophryne* Boettger 1895 (at least 29 species) are considered here (Johnston & Richards 1993; Kraus & Allison 2000, 2006, 2009a,b; Allison & Kraus 2003; Zweifel 2003; Menzies 2006; Günther 2006, 2010; Richards & Oliver 2007, 2010; Günther *et al.* 2009; Kraus 2010).

In Australia, Asterophryinae is represented by *Cophixalus* and *Austrochaperina* (cf. Zweifel 2000 for use of *Austrochaperina* rather than *Sphenophryne*). Together they constitute 54% of rainforest-restricted frog species in the Wet Tropics region of north Queensland, Australia where most species have small, often fragmented distributions (Hoskin 2004). Their concentration in this biologically highly significant region has made the group a focus