

REVIEW ARTICLE

# Ontogenetic diversity and early development of frogs in the South American family Cycloramphidae

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## Abstract

**Ontogenetic diversity and early development of frogs in the South American family Cycloramphidae.** Literature describing peculiarities of development in cycloramphid frogs is reviewed. This study reports data on sizes and pigmentation of eggs, the morphology of early cleavage, sites of embryo and tadpole development (in water or on land), larval nutrition (exotrophic or endotrophic), and the occurrence of brooding. Despite the moderate number of species, this family is ontogenetically diverse, with repeated modifications of ontogenesis. The focus is on the development of frogs in the genus *Rhinoderma*, the early cleaving embryos of which are less modified than early embryos of many other frogs. The peculiarities of development in the family Cycloramphidae are compared with those in representatives of other families of anurans.

**Keywords:** Anura, cleavage, diversity, evolution of development, *Rhinoderma*, South America.

## Resumo

**Diversidade ontogenética e desenvolvimento inicial nos anuros sulamericanos da família Cycloramphidae.** Revisei a literatura que descreve as peculiaridades do desenvolvimento dos anuros da família Cycloramphidae. Este estudo fornece dados sobre tamanho e pigmentação dos ovos, morfologia das clivagens iniciais, locais de desenvolvimento dos embriões e girinos (aquáticos ou terrestres), nutrição larval (exotrófica ou endotrófica) e ocorrência de incubação dos ovos. Apesar do número moderado de espécies, essa família é muito diversificada ontogeneticamente, com modificações repetidas na ontogenia. O foco está no desenvolvimento dos anuros do gênero *Rhinoderma*, cujos embriões precoces são menos modificados que os de muitos outros anuros. Comparei as peculiaridades do desenvolvimento na família Cycloramphidae com as de representantes de outras famílias de anuros.

**Palavras-chave:** América do Sul, Anura, clivagem, diversidade, evolução do desenvolvimento, *Rhinoderma*.

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## Introduction

Anura comprises 38 families and 5996 species (AmphibiaWeb 2011). Although the Neotropical frog fauna is the richest and most diverse, there have been embryological studies of only a few taxa of this fauna—i.e., representatives of Dendrobatidae, Eleutherodactylidae, Hemiphraclidae, and Leiuperidae (Elinson and del Pino 1985, Townsend and Stewart 1985, Callery *et al.* 2001, del Pino *et al.* 2004, 2007, Desnitskiy 2004, Romero-Carvajal *et al.* 2009).

The extent of ontogenetic diversity (Duellman 1985, Haddad and Prado 2005) is variable among families of anurans. For instance, in the third largest family of anurans, Strabomantidae (572 species), as well as in several other families of Neotropical frogs, all members are terrestrial breeders and direct developers (Hedges *et al.* 2008, Heinicke *et al.* 2009). In contrast, in the relatively small South American frog family, Cycloramphidae (105 species; Correa *et al.* 2006, Frost *et al.* 2006), there is considerable ontogenetic diversity. Therefore, it may be of interest to review published data and compare developmental patterns in this family with those of frogs from other families. The review is intended to stimulate further research in the field of comparative embryology (developmental biology) of the cycloramphid frogs.

Approximately 50% of cycloramphid species from temperate or tropical latitudes (representatives of the genera *Hylorina*, *Insuetophrynus*, *Limnomedusa*, *Macrogenioglottus*, *Odontophrynus*, *Proceratophrys*, *Rupirana*) deposit pigmented eggs with diameters of 1–2.5 mm in lentic or lotic waters and have an exotrophic tadpole stage (Díaz *et al.* 1983, Haddad and Prado 2005, Cárdenas-Rojas *et al.* 2007, Giaretta and Facure 2008, Juncá and Lugli 2009, Kaefer *et al.* 2009). The number of eggs in a clutch varies interspecifically from about 100 to several thousand. However, descriptions of the morphological features of early cleavage and blastula formation are absent from the literature. In this context, it is appropriate to point out that the “standard”

biphasic anuran development usually includes a series of 10–12 synchronous cleavage divisions in the pigmented animal hemisphere of early embryos. This is characteristic of the species with relatively small eggs (diameters of 1.2–2.5 mm), such as the South African clawed frog *Xenopus laevis* from the family Pipidae (Dettlaff and Rudneva 1975, Newport and Kirschner 1982) or numerous representatives of the families Ranidae and Bufonidae from the temperate latitudes of the Northern Hemisphere (Pollister and Moore 1937, Gosner 1960). Although future studies may reveal a similar cleavage pattern in some cycloramphids, this paper deals principally with various deviations from the standard anuran development in Cycloramphidae.

## Development of *Rhinoderma*

The embryology of *Rhinoderma* is perhaps the best known of all cycloramphids. Members of this genus inhabit temperate and austral forests of central and southern Chile and adjacent Argentina, and are characterized by an unusual form of parental care; embryos carried in the male’s vocal sac. Early embryological studies (Jorquera *et al.* 1972, 1974) demonstrated considerable developmental variation in different populations of *Rhinoderma darwini*, but subsequently, it was shown that these researchers had dealt with two different species, *R. darwini* and *R. rufum* (Formas *et al.* 1975, Formas 1976).

*Rhinoderma darwini* deposits 3–20 pigmented, yolk-rich eggs with a diameter of 4 mm in the leaf litter. After external fertilization, the male remains near the clutch for about 20 days (Jorquera *et al.* 1972, 1982, Crump 2002, Busse 2003). When the first signs of embryonic muscular activity become visible, the male picks the embryos up and stores them in his vocal sac, where the tadpoles hatch within 3 days. After about 50 days of brooding in the vocal sac, the tadpoles metamorphose and tiny froglets exit through the male’s mouth.

The larva of *darwini* has a poorly developed caudal fin and lacks external gills, a spiracle, a

beak and cornified teeth; the duodenal epithelium differentiates only at the final stages of larval life (Jorquera *et al.* 1972, 1982). Experimental investigations have confirmed the existence of a trophic relationship between the male and the larvae (Garrido *et al.* 1975, Goicoechea *et al.* 1986). Nutrients are transferred from paternal to larval tissues; the internal epithelium of the vocal sac exhibits secretory activity and the superficial cells of the larval skin contain pinocytotic vesicles.

In *Rhinoderma rufum* (Jorquera *et al.* 1974, 1982), a clutch contains 12–24 pigmented eggs with a diameter of 2.4 mm laid on moist ground. The first muscular activity occurs after 8 days, when the embryos are transferred to the male's vocal sac. The brooding period is relatively short, occupying only 2 wk, after which the male releases the tadpoles into temporary pools (Formas *et al.* 1975). The duration of free-swimming larval period has not been determined. In contrast to larvae of *R. darwinii*, the young tadpoles of *R. rufum* possess the usual features of free-living exotrophic anuran larvae—viz., external gills, a spiracle, a larval mouth with horny beak and teeth; the tail fin is well developed.

Jorquera *et al.* (1974, 1982) suggested that the type of development in *Rhinoderma rufum* might be intermediate between the more derived type of *R. darwinii* and the ancestral, biphasic anuran development. Molecular-phylogenetic study of the genus *Rhinoderma* might provide a framework for a well-founded interpretation of the ontogenetic evolution in these frogs. Unfortunately, *R. rufum* has not been seen in nature in recent years and there are reasons to believe that the species is critically endangered or even extinct.

It is of interest to compare morphological and chronological data on the early stages of embryogenesis in *Rhinoderma darwinii* (Jorquera *et al.* 1972) and *R. rufum* (Jorquera *et al.* 1974). These are the only two cycloramphids for which tables of normal development have been published. At 18°C, *R. rufum* develops more rapidly than *R. darwinii*; thus, gastrulation starts

approximately 54 h and 103 h after egg laying, respectively. The morphological features of early cleavage and blastula formation are rather similar in both species (except the larger egg diameter in *R. darwinii*). As a result of the third (latitudinal) cleavage division, differentiation into small animal and large vegetal blastomeres occurs. The synchrony of divisions is lost after the 16-celled stage.

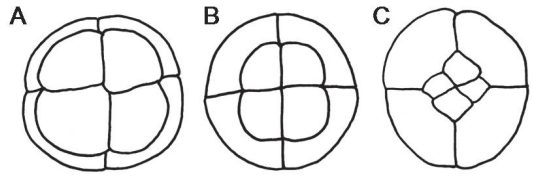
It is of interest to compare the eight-blastomere stage of embryos of *R. rufum*, *Xenopus laevis* (Pipidae) and *Heleioporus eyrei* (Australian Myobatrachidae) (Figure 1). Egg deposition and embryogenesis occur on land in the latter species, but the exotrophic tadpoles live in water (Packer 1966). The difference in sizes of the animal and vegetal blastomeres at the eight-celled stage of cleavage in *R. rufum* is greater than in *X. laevis*, but much less than in *H. eyrei*. Note that in *Gastrotheca riobambae* (a marsupial frog from Hemiphractidae), early embryos develop in a pouch on the female's back and the process of cleavage is characterized by a maximal deviation from the standard development. The third cleavage division, like the two preceding divisions, is longitudinal (meridional) and so at the eight-celled stage there is no differentiation into animal and vegetal blastomeres (del Pino and Looz-Vela 1990). Therefore, despite the unusual reproductive biology and development in *Rhinoderma*, the morphology of their early embryos is more like that of "typical" anuran embryos than might have been expected. This may be explained by the fact that in both species of *Rhinoderma*, brooding begins only after early embryogenesis has been completed, rather than immediately after fertilization as in *G. riobambae*.

It is difficult to compare the development of *Rhinoderma* with that of recently extinct gastric brooding myobatrachid frogs of the genus *Rheobatrachus*, because there are no appropriate data for the latter genus. However, *Rhinoderma* can be compared with another myobatrachid, the marsupial frog *Assa darlingtoni* (Ehmann and Swan 1985). The jelly-like clutch of *Assa* contains 10–18 fertilized eggs with a diameter of

2.5 mm; the embryos develop during first 11 days on land under the protection of the female. After hatching, eyeless, endotrophic larvae with a great reserve of yolk, wriggle into inguinal pouches of the male. In about 2 months, the miniature froglets emerge. The development of this species seems to have more features in common with *R. darwinii*, than with *R. rufum*. Unfortunately we cannot determine whether the early cleavage of *Assa* deviates from the “standard pattern of anuran cleavage” more than that of *Rhinoderma* because no one has yet described the morphology of early embryos in *Assa darlingtoni*.

#### Ontogeny of *Eupsophus*, *Thoropa*, *Cycloramphus* and *Zachaenus*

Frogs of the genus *Eupsophus* also occur in the temperate and austral forests in Argentina and Chile. The clutch usually contains 50–100 unpigmented, yolk-rich eggs with a diameters of 2.8–7.2 mm. Development is endotrophic and up to the completion of metamorphosis occurs in dark conditions, in water-filled chambers or cavities in the ground or in the small volume of water under moss and stones (Formas and Vera 1980, Vera Candioti *et al.* 2005, 2011). Despite the endotrophic development, the tadpoles of *Eupsophus* retain a number of ancestral features of the exotrophic tadpoles of anuran amphibians; they have differentiated mouthparts and are active swimmers, as evidenced by the well-developed caudal fin (Nuñez and Úbeda 2009). The genus *Eupsophus* may represent an example of an initial step toward the origin of the endotrophic development in frogs, given the accumulation of a large amount of yolk in the egg; a reduction of mouthparts might be the next step. The deviations from standard frog development in representative cycloramphids that live in the temperate and austral forests of South America may be associated with a transition to terrestrial breeding and brooding of progeny in the paternal vocal sac (*Rhinoderma*) or with the deposition of large, yolk-rich eggs in a small volume of water (*Eupsophus*).



**Figure 1.** Schematic representation of early embryos in three species of frogs at the eight-blastomere stage viewed from the animal pole. (A) *Xenopus laevis* (adapted from Dettlaff and Rudneva 1975). (B) *Rhinoderma rufum* (adapted from Jorquera *et al.* 1974). (C) *Heleioporus eyrei* (adapted from Packer 1966). Egg diameters in *X. laevis*, *R. rufum*, and *H. eyrei* are 1.3–1.4 mm, 2.4 mm, and 2.6–2.9 mm, respectively.

Let us turn to the development of some Cycloramphidae living in the warm, humid climate of southeastern Brazil. *Thoropa miliaris* deposits 750–1000 pigmented eggs with a diameter of 1.7 mm on the ground near streams. The exotrophic tadpoles are semiterrestrial (semiaquatic); they live at the transition between land and flowing water, or are found on rocks over which a shallow film of water flows (Giaretta and Facure 2004, Haddad and Prado 2005). A similar development with exotrophic, semiterrestrial tadpoles characterizes several species of the genus *Cycloramphus*—e.g., *C. dubius*, though its clutch contains only 30–80 weakly pigmented eggs with a diameter of 3 mm (Giaretta and Cardoso 1995). In contrast, in several other members of the same genus (e.g., *C. faustoi* and *C. stejnegeri*), approximately 30 large, unpigmented eggs with a diameter up to 4 mm are laid on the forest floor. When the larvae hatch, they continue their endotrophic development on the ground or back of one of the parents (Haddad and Prado 2005, Brasileiro *et al.* 2007). *Zachaenus parvulus* (= *Oocormus microps*) is of great interest. Its eggs are very large (diameter 6 mm) and yolk-rich. After hatching, the tadpoles are relatively immobile and remain in a terrestrial nest; the period of endotrophic larval life is about 17 days (Lutz 1943, 1947). Note that with respect to ontogenesis,

*Zachaenus* seems to resemble the Australian myobatrachids *Philoria* (*Kyarranus*) *sphagnicolus*, *Crinia* (*Bryobatrachus*) *nimbus*, and *Geocrinia vitellina*; the endotrophic and relatively immobile tadpoles of these taxa also develop in terrestrial nests (de Bavay 1993, Mitchell 2001, 2002, Desnitskiy 2010).

Unfortunately, published morphological descriptions of the early stages of embryogenesis in *Eupsophus*, *Thoropa*, *Cycloramphus*, and *Zachaenus* are lacking. It would be useful if anuran researchers directed their attention to this topic in the future (including the preparation of tables for the normal development of several selected species).

### Concluding remarks and perspectives

Currently, we cannot classify developmental types in the South American family Cycloramphidae as clearly as has recently been done for the Australian Myobatrachidae (Desnitskiy 2010). However, it is relevant to regard *Rhinoderma darwini*, *Cycloramphus faustoi* (or *C. stejnegeri*), and *Zachaenus parvulus* as examples of maximal deviation from the ancestral biphasic life cycle in Cycloramphidae. The genera *Rhinoderma*, *Cycloramphus*, and *Zachaenus* demonstrate different versions of independent transitions to the endotrophic terrestrial development. However, direct-developing cycloramphids (with a complete absence of larval stage) have not yet been discovered. Perhaps this is because members of this family coexist with numerous direct-developing species from other families of South American anurans in the same tropical territory (southeastern Brazil) (Heyer 1975, Haddad and Prado 2005, Giaretta and Facure 2008, Hedges *et al.* 2008). In contrast, the climate of temperate forests of Argentina and Chile, where the genera *Eupsophus* and *Rhinoderma* dwell, seems incompatible for the life of direct-developing frogs; a similar situation occurs in the temperate latitudes of the Northern Hemisphere.

Further developmental studies of the terrestrial breeding and/or endotrophically developing

cycloramphids, such as *Cycloramphus*, *Eupsophus*, *Rhinoderma*, *Thoropa*, and *Zachaenus*, are necessary. Furthermore, the genera *Alsodes* and *Insuetophrynus*, the embryos and exotrophic tadpoles of which develop in cold streams (Diaz *et al.* 1983, Formas and Brieva 2004) are particularly intriguing. However, for an embryologist, any cycloramphid is of interest. It is appropriate to remind the reader that tables of normal development are currently available only for two species of *Rhinoderma*; thus, the comparative embryology of this ontogenetically diverse frog family has great potential.

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