repatterning in direct-developing frogs

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SUMMARY

The Puerto Rican direct-developing frog *Eleutherodactylus coqui* (Leptodactylidae) displays a novel mode of jaw muscle development for anuran amphibians. Unlike metamorphosing species, several larval-specific features never form in *E. coqui*; embryonic muscle primordia initially assume an abbreviated, mid-metamorphic configuration that is soon remodelled to form the adult morphology before hatching. Also lacking are both the distinct population of larval myofibres and the conspicuous, larval-to-adult myofibre turnover that are characteristic of muscle development in metamorphosing species. These modifications are part of a comprehensive alteration in embryonic cranial patterning that has accompanied life history evolution in this highly speciose lineage. Embryonic 'repatterning' in *Eleutherodactylus* may reflect underlying developmental mechanisms that mediate the integrated evolution of complex structures. Such mechanisms may also facilitate, in organisms with a primitively complex life cycle, the evolutionary dissociation of embryonic, larval, and adult features.

1. INTRODUCTION

Direct development is a novel reproductive mode in Recent amphibians. It is characterized by evolutionary loss of the free-living, aquatic larval stage typical of metamorphosing species; embryogenesis culminates in the birth of a fully formed, juvenile frog, salamander, or caecilian. Direct development has evolved independently in each of the three living orders and is characteristic of many hundreds of extant species (Wake 1989). Indeed, it is the predominant reproductive mode in some large clades, e.g. plethodontid salamanders (Wake & Hanken 1996), and probably evolved at least ten times in anurans alone (Duellman & Trueb 1986). Direct development can have important ecological and evolutionary consequences. These range from loss of the need for aquatic breeding sites (McDiarmid 1978), to release from larval constraints on adult morphology associated with the ancestral, metamorphic ontogeny (Alberch 1987, 1989; Wake & Larson 1987; Wake & Roth 1989). Yet, consequences of the evolution of direct development for the developmental biology of individual taxa are poorly known (Elinson 1990; Elinson *et al.* 1990; Wake & Marks 1993). This is especially true for those features whose modification may affect the evolutionary success and diversification of particular lineages (Alberch 1987, 1989).

We examined embryonic development of the jaw musculature in the Puerto Rican frog *Eleutherodactylus coqui* (Leptodactylidae; figure 1) to assess the consequences of direct development for these and other cranial tissues. We focused on the muscles responsible for mouth opening and related movements in frogs. There are five such muscles in the larvae of most families, including the Leptodactylidae (Starrett 1973; figure 2*a*,*b*). All five muscles are derived from the second embryonic (hyoid) arch and are innervated by the seventh cranial (facial) nerve (Edgeworth 1935). At metamorphosis these larval muscles coalesce to form the depressor mandibulae, the single, complex jaw-opening muscle found in all adult frogs (De Jongh 1968). This reorganization entails shifts in muscle origin to as many as three sites within the head and insertion to the posterior tip of the mandible. Accompanying these changes in muscle number, size, orientation and attachment is myofibre turnover: larval myofibres degenerate and are replaced by adult myofibres recruited from satellite cells within the larval muscles (De Jongh 1968). These conspicuous, qualitative changes in muscle morphology, which accompany metamorphosis in species displaying the

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