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Identification and evolution of molecular domains involved in differentiating the cement gland-promoting activity of Otx proteins in *Xenopus laevis*

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ABSTRACT

Otx genes are a class of vertebrate homeobox genes, homologous to the *orthodenticle* gene of *Drosophila melanogaster*, that play a crucial role in anterior embryo patterning and sensory organ formation. In the frog, *Xenopus laevis*, at least three members of this class have been isolated: *otx1*, *otx2* and *otx5* (*crx*); they are involved in regulating both shared and differential processes during frog development. In particular, while *otx2* and *otx5* are both capable to promote cement gland (CG) formation, *otx1* is not. We performed a molecular dissection of Otx5 and Otx1 proteins to characterize the functional parts of the proteins that make them differently able to promote CG formation. We show that a CG promoting domain (CGPD) is localized at the Otx5 C-terminus, and is bipartite: CGPD1 (aa 210–255) is the most effective domain, while CGPD2 (aa 177–209) has a lower activity. A histidine stretch disrupts CGPD1 continuity in Otx1 determining its loss of CG promoting activity; this histidine-rich region acts as an actively CG repressing domain. Another Otx1 specific domain, a serine-rich stretch, may also be involved in repressing Otx1 potential to trigger CG formation, though at a much lower level. This is the first evidence that these domains, specific of the Otx1 orthology group, play a role during development in differentiating Otx1 action compared to other Otx family members. We discuss the potential implications of their appearance in light of the evolution of Otx functional activities.

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1. Introduction

Otx genes are a class of vertebrate paired-like K_{50} homeobox genes (Galliot et al., 1999) related to the *orthodenticle* gene of *Drosophila melanogaster*, which plays a crucial role in the development of the fly nervous system and sensory structures (Cohen and Jurgens, 1990; Finkelstein et al., 1990). Similarly, Otx genes are essential for anterior central nervous system (CNS) and sensory organ formation (Acampora et al., 1995, 1996; Acampora and Simeone, 1999; Freund et al.,

1997; Furukawa et al., 1997; Martinez-Morales et al., 2001). In the frog, *Xenopus laevis*, at least three members of the Otx class have been isolated: *otx1*, *otx2*, and *otx5* (*crx*) (Blitz and Cho, 1995; Kablar et al., 1996; Kuroda et al., 2000; Pannese et al., 1995; Vignali et al., 2000).

During early phases of *Xenopus* embryogenesis, *otx* genes are expressed in the developing head tissues (rostral CNS: forebrain and midbrain; anterior endomesoderm of the head organizer) that do not undergo convergent extension movements. Misexpression of these genes by mRNA microinjection

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