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Spatio-temporal expression of *Sox* genes in murine palatogenesis

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ABSTRACT

Members of the *Sox* gene family play critical roles in many biological processes including organogenesis. We carried out comparative *in situ* hybridisation analysis of seventeen *Sox* genes (*Sox1-14*, *17*, *18* and *21*) during murine palatogenesis from initiation to fusion of the palatal shelves above the dorsal side of the tongue. At palatal shelf initiation (E12.5), the localized expression of six *Sox* genes (*Sox2*, *5*, *6*, *9*, *12* and *13*) was observed in the shelves, whereas *Sox4* and *Sox11* showed ubiquitious expression. During the down-growth of palatal shelves (E13.5), *Sox4*, *Sox5*, and *Sox9* exhibited restricted expression to the interior side of the palatal shelves facing the tongue. Following elevation of the palatal shelves (E14.5), *Sox2*, *Sox11* and *Sox21* expression was present in the midline epithelial seam. We thus identify dynamic spatio-temporal expression of *Sox* gene family during the process of palatogenesis.

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1. Introduction

Cleft palate is one of the most common congenital birth defects in humans, suggesting that palatogenesis is easily perturbed by genetic and environmental factors (Gritli-Linde, 2007; Dixon et al., 2011; Iwata et al., 2011). Many molecules have been identified in palatogenesis, which requires fine tuning in terms of the timing, location and size of their expression for normal palate development (Murray and Schutte, 2004; Smith et al., 2013; Meng et al., 2009; Bush and Jiang, 2012; Gritli-Linde, 2007; Iwata et al., 2011; Dixon et al., 2011). The secondary palate initiates as the formation of palatal shelves that emerge from the internal side of the maxillary arch. The palatal shelves are composed of mesenchyme derived mainly from the neural crest and a thin layer of oral epithelium (Ito et al., 2003). The secondary palate develops through sequential and reciprocal interactions between the epithelium and mesenchyme, and involves multiple developmental events such as growth, elevation and fusion (Murray and Schutte, 2004; Smith et al., 2013; Meng et al., 2009; Bush and Jiang, 2012; Gritli-Linde, 2007; Iwata et al., 2011; Dixon et al., 2011). The growing bilateral palatal shelves extend downward beside the developing tongue, and then elevate above the dorsal side of the tongue. Following elevation, the paired palatal shelves grow horizontally towards each other to meet along the midline. The midline epithelial seam (MES) is formed at this junction, and disappears allowing the fusion of the palatal shelves with mesenchymal confluence. It has been shown that many genes are differentially expressed along the anterior-posterior axis in the developing palate (Li and Ding, 2007; Bush and Jiang, 2012). Distinct shapes have also been reported in developing palatal shelves along the same axis (Yu and Ornitz, 2011). This suggests that distinct molecular mechanisms are present in palatogenesis along the anterior-posterior axis.

Sox proteins are characterized by a highly conserved DNA binding motif and high mobility group (HMG) domain. Twenty *Sox* genes have been identified in mice. Members of the *Sox* gene family

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show dynamic and diverse expression patterns during development. Mutation analyses in mice provide evidence that they play multiple roles during development (Pevny and Lovell-Badge, 1997; She and Yang, 2015). Although mutation in *Sox2*, *Sox5*, *Sox9* and *Sox11* has been shown to result in cleft palate in human and/or mouse, the expression of the *Sox* family members – including *Sox2*, *Sox5*, *Sox9* and *Sox11* – in palate development remains unclear (Male et al., 2002; Langer et al., 2014, 2014; Sock et al., 2004; Bi et al., 2001; Mori-Akiyama et al., 2003; Smits et al., 2001).

We therefore carried out comparative *in situ* hybridisation analysis of seventeen *Sox* genes (*Sox1-14*, *17*, *18* and *21*) during murine palatogenesis. Here, we identify the dynamic spatio-temporal expression of *Sox* genes in palatal development.

2. Results

Since distinct molecular mechanisms are present in palatogenesis along the anterior-posterior axis, we examined expression of the *Sox* gene family in the palatal tissues of the anterior, middle and posterior regions.

Neither *Sox1* nor *Sox3* expression could be detected in palatal shelves from embryonic day (E) 12.5 to E14.5 (data not shown).

In mice, the secondary palate initiates as palatal shelves that emerge at E12.5 from the internal side of maxillary arch. *Sox2* showed strong expression in the epithelium of the palatal shelves (Fig. 1A–C). *Sox4* was ubiquitously expressed in the maxillary arch, while its expression was slightly weaker in palatal shelf mesenchyme (Fig. 1D–F). *Sox5* exhibited restricted expression in the presumptive maxillary bone region (Fig. 1G–I). *Sox6* was expressed in the epithelium of the palatal shelves, while it also showed restricted expression in the presumptive maxillary bone region (Fig. 1J–L). *Sox8* expression could not be detected in the palatal shelves at E12.5 (Fig. 1M–O). *Sox9* exhibited restricted expression in the presumptive maxillary bone region (Fig. 2A–C). *Sox11* showed ubiquitous expression in the maxillary arch (Fig. 2D–F). No expression of *Sox12* was observed in developing palatal shelves

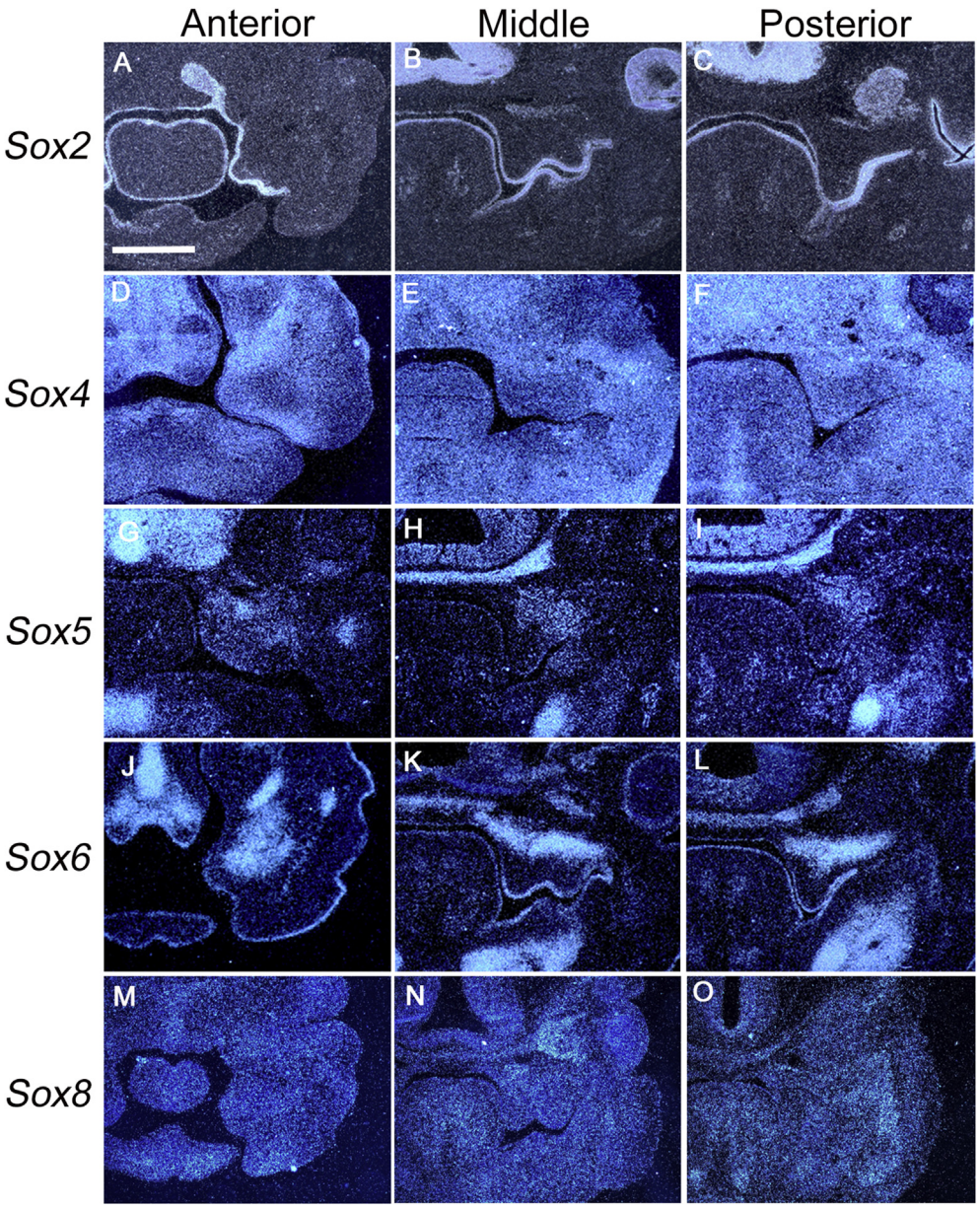

Fig. 1. The expression of *Sox* (*2, 4, 5, 6, 8*) genes in rodent palatal development at E12.5. *In situ* hybridisation of *Sox2*, *Sox4*, *Sox5*, *Sox6* and *Sox8* on anterior (A,D,G,J,M), middle (B,E,H,K,N) and posterior (C,F,I,L,O) frontal head sections at E12.5. Scale bars: 500 μm.

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