

Position-Specific Expression of Homeoprotein Gradients in Different Feather Tracts^a

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Homeoproteins have been shown to be expressed in defined bands along the anterior-posterior (A-P) body axis and are involved in determining the patterns of insect appendages.¹ In vertebrates, homeoproteins are also expressed in anterior-posterior (A-P) gradient in the spinal cord. Recently, homeoproteins were also shown to be distributed in a gradient in developing limb buds^{2,3} and feather buds,⁴ thus suggesting that homeoproteins may be involved in setting up the A-P axes of cell fields at different levels, first for the body axis, then for the limb axis, and finally for the feather axis.⁴ Here, we further examine the orientation of the homeoprotein gradient at the level of the feather tract using the procedure of Chuong *et al.*⁴ We found that there are different but definite gradient axes in different tracts. Thus there is a position-specific homeoprotein expression pattern in each feather bud. Together with previous findings,⁴ the observations are summarized as follows.

1. Some homeoproteins are expressed in the mesoderm of feather buds. The concentration of homeoproteins in an individual feather bud varies, depending on its position in a particular feather tract. Using *XIHbox 1* as an example, *XIHbox 1* is all over the mesoderm in some buds, yet not detected at all in other buds. The rest of the buds have different degrees of gradient distribution of *XIHbox 1*. (FIG. 1, patterns 1–4). There is an orderly transition of these expression patterns across the feather tract. Thus there is a global homeoprotein gradient spreading over each feather tract (FIG. 1).
2. The orientations of homeoproteins in different feather tracts are different and are not always parallel to the body axis. For example, the maximal expression of *XIHbox 1* in the spinal tract is in the scapular region and is parallel with the body axis. But the maximal expression of *XIHbox 1* in the wing feathers is in the anterior-proximal region of the wing and the axis is not parallel with the body axis (FIG. 1).
3. Within some feather buds, there are minute homeoprotein gradients. The orientations of homeoprotein gradients vary. For *XIHbox 1*, it is expressed higher in the anterior of the developing feather buds and decreases toward the posterior end (Ref. 4 and FIG. 1, patterns 2 and 3). Other homeoproteins, such as *Hox 5.2*, may have a different orientation.⁴ A bud can have different expression patterns for different homeoproteins. For example, a bud from the

^aThis work was supported by National Institutes of Health Grant HD 24301 and by the Council for Tobacco Research. C.-M.C. is a recipient of an American Cancer Society Junior Faculty Research Award.

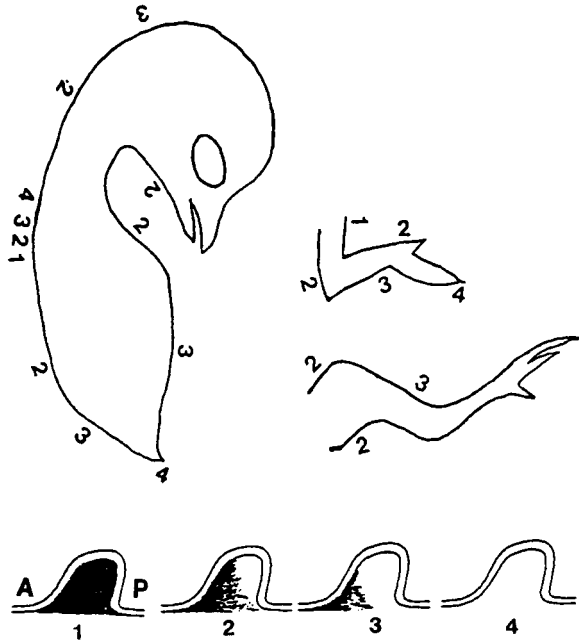


FIGURE 1. Mapping the orientation of the homeoprotein gradients in different feather tracts. A schematic chicken embryo is marked with numbers representing different patterns of XIHbox 1 expression. Pattern 1, buds with the homeoprotein all over the mesoderm cells. Pattern 2, buds with the homeoprotein gradient passing over the anterior (A)–posterior (P) midline of the bud. Pattern 3, buds with the homeoprotein gradient not passing over the A-P midline of the bud. Pattern 4, buds with no detectable homeoprotein in the mesoderm. The left side of the numbers that indicate the expression pattern of homeoproteins are at the anterior portion of the feather bud. The distance between these numbers reflects the slope of the global tract gradient. In the spinal tract (interscapular–dorso-pelvic⁶), the highest expression is at the scapular region. There is a decrease in XIHbox 1 expression toward both the neck and the tail regions. In the abdominal tract (sternal-medial abdominal⁶), the “tract gradient” decreases in a very shallow slope. In the wing tract, the highest expression is in the proximal-anterior region of the wing. No expression is at the distal tip. In contrast, Hox 5.2 is still expressed in pattern 3 at the wing tip. The orientation of the tract gradient in the wing is in agreement with the distribution of XIHbox 1 in the limb bud mesoderm.²

tail region expresses pattern 4 (as defined in FIG. 1) for XIHbox 1 and pattern 3 for Hox 5.2.

4. The feather mesoderm has different origins. For buds on the trunk, the feather mesoderm are from the somite; for those on the wing, they are from the somatopleure; and for those on the head, they are from the cranial neural crest. Despite the difference in the origin of embryological germ layers, the XIHbox 1 gradients are present on the mesoderm of all these feather buds.
5. Some homeoproteins, such as XIHbox 1 but not Hox 5.2, are also present in the developing ectoderm. XIHbox 1 appears to be evenly distributed in the ectoderm throughout the body.

Different types of cutaneous appendages form on the skin. The feathers from the trunk, wing, and tail have distinct structures. During development, each feather bud appears to express a combination of homeoproteins, and this specific expression pattern may be one of the determining factors specifying the type of cutaneous appendages to be formed. Classical transplantation experiments have shown that pattern determination factors reside in the mesenchyme,⁵ which is consistent with the above hypothesis. Experimental perturbation of homeoprotein expression may thus lead to the malformation or ectopic formation of cutaneous appendages as those seen in the insect.¹ We are currently testing these possibilities.

ACKNOWLEDGMENTS

I thank Dr. Eddy M. De Robertis of U.C.L.A. for antibodies to XIXbox 1 and Hox 5.2, and Ms. Sheree A. Ting for technical assistance.

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