



Figure 10.7. Representation of the vertebrae and somites of the chick (*top*) and the mouse (*bottom*) showing the anterior boundary of expression of *Hox* genes. C, T, L, S, and C refer respectively to the cervical, thoracic, lumbar, sacral, and caudal regions of the vertebral column. Modified from *Development* (Burke et al., vol. 121, 1995), Company of Biologists Ltd.

ic vertebra (T-1). Ribs are expressed in the thoracic but only rarely in the cervical region, and the transverse and dorsal processes are much larger. In thirty-one of the seventy-two homozygotes in which *Hoxa-6* was disrupted, a rib characteristic of the thoracic region was expressed on the last cervical. Other aspects of the last cervical vertebra were not modified, but the neural spine on the most anterior thoracic vertebra assumed the larger size normally seen in the second thoracic.

These studies provide extensive information on the specific areas of expression of the paralogues of various *Hox* groups. Each paralogue may control the expression of particular structural details within a single bone, but there is also considerable overlap and potential redundancy in more general aspects of bone formation. Loss of function in some *Hox* genes may result in only minor changes in the anatomy of particular bones without serious reduction in viability and fecundity, but loss of other genes, which also control other systems, may be fatal.

Although disruption of *Hox* genes may aid in determining the function of their normal counterparts, it is unlikely to contribute to understanding normal evolutionary processes. The presence of exactly the same number and arrangement of all the *Hox* genes in modern birds and mammals, despite these groups having separated from one another phylogenetically at least 300 million years ago, points to their extremely conservative nature. There is no evidence that any *Hox* genes have been lost since the much earlier divergence of actinopterygian and sarcopterygian fish, sometime in the Silurian. It is thus very unlikely that total loss of function of any *Hox* gene has played a role in small-scale anatomical changes among modern vertebrate groups. On the other hand, changes in the regulation of *Hox* genes, including altering or even eliminating their effect on other genes, might have results similar to those reported in these experiments.

The evolution of fins and limbs

Changes in the structure of the fins of fish and the limbs of tetrapods are among the most striking aspects of vertebrate evolution. They directly reflect changes in habi-