

Developmental processes and the evolution of the skull and axial skeleton

The origin of new developmental processes, especially those involving the neural crest cells and placodes, played a major role in the establishment of the major features of the vertebrate skull. On the other hand, although much is known of how developmental processes affect the ontogeny of modern vertebrates (e.g., *The Skull*, Hanken and Hall 1993), it has been much more difficult to associate subsequent phylogenetic change with alterations in particular developmental processes. This may be partially due to the fact that genes of the *Hox* cluster, which are so useful in the study of developmental processes in other parts of the body, are expressed only in the most posterior part of the skull, associated with the hindbrain and the branchial arch region (Thorogood 1993). The remainder of the skull is completely remodeled through the activity of the neural crest cells and placodes, which appear to overlay any more primitive patterning that may have existed in earlier chordates. As recently as 1993, Hanken and Thorogood wrote: "Virtually nothing, however, is known about the role of homeobox genes in cranial evolution following the initial origin of the head" (p. 13).

Another reason that it has been difficult to associate changes in processes of development with the evolution of the head region among vertebrates is the sheer complexity of the system, with a three-dimensional expression of a host of different tissues, all of which have their own patterns of developmental control. In addition, most studies of cranial development have concentrated on particular species of birds and mammals, rather than investigating the broad spectrum of different cranial patterns illustrated by different major groups of fish, amphibians, and the modern reptile orders.

Two other areas of the vertebrate body, the axial skeleton and the limbs, provide much simpler, essentially one- and two-dimensional systems whose development has been studied in a wider range of taxa. They show in considerable detail how changes in the pattern of expression of particular genes, especially those of the *Hox* cluster, are associated with specific differences in developmental processes and adult morphology.

The thirteen *Hox* groups of all four clusters are expressed in a linear fashion in spatially restricted domains from the head to the end of the tail. They are expressed in a variety of tissues, including hindbrain segments, branchial arches, neural tube, neural crest, paraxial mesoderm, limbs, surface ectoderm, gut, and gonadal tissues (Krumlauf 1994). The regions of expression of different *Hox* groups and different paralogues within each group is clearly shown in different regions of the vertebral column (Burke et al. 1995).

Burke and her colleagues investigated the expression of *Hox* genes in several animals that exhibit clear differences in the relative number of vertebrae in the cervical, thoracic, lumbar, and sacral regions. They concentrated on the well-known laboratory mouse and the chick, but also studied the frog *Xenopus* and the goose. They found that the anterior limit of *Hox* expression was associated with the morphology of the vertebral regions rather than with the vertebral number (Fig. 10.7).

Hox groups 1–3 are expressed in the hindbrain and the occipital somites, whereas groups 4 and 5 have anterior boundaries of expression within the cervical region. Boundaries of expression of *Hox-4* genes are similar in mouse and chick,