

ticularly dramatic. Although *Branchiostoma* has a light-sensory structure and an organ of balance, these show few of the specialized characteristics of the vertebrate eyes or inner ear, and the anterior portion of the neural tube is only slightly expanded, without any of the derived features of the vertebrate brain. It is these characteristics of the head region that most clearly distinguish even the most primitive fossil and living vertebrates from nonvertebrate chordates. For this reason, many biologists prefer "craniate" rather than "vertebrate," since none of the primitive fish groups have vertebrae.

This view of the origin of vertebrates as being specifically associated with the origin of cranial structures was strongly emphasized by Northcutt and Gans (1983) and Gans (1989, 1993). They pointed out that nearly all of the specifically craniate features of the head region develop from a unique set of tissues: the sensory placodes and the neural crest cells. No comparable tissues are known in any of the nonvertebrate chordates. The *sensory placodes* are restricted to the head region (except for those that develop into the lateral line canals) and are primarily associated with the development of the olfactory, optic, and otic capsules, and chemical sensory structures within the oral cavity. The *neural crest cells* originally proliferate at the junction of the developing neural tube and the adjacent ectoderm, posterior to the skull; however, these cells are migratory and contribute significantly to structures throughout the head region as well as the trunk. Expression of the *premature death* mutation in both sensory placodes and neural crest tissue suggests that these tissues had a common phylogenetic and developmental history (Smith, Graveson, Hall 1994).

Gans and Northcutt (1983) argued that the brain and sensory structures of the head region in craniates evolved anterior to the end of the nerve cord in cephalochordates, forming what amounts to a new head. This was based on the fact that the notochord extends to the very end of the neural tube in *Branchiostoma*, in contrast to its more posterior termination in all vertebrates. In addition, the pattern of segmentation in the head region of craniates seems very different from that of the trunk, and much of the bone and muscle tissue in the head is derived from neural crest cells rather than from mesodermal somites, as is the case in the trunk region.

Subsequently, Holland et al. (1992) identified one of the *Hox* genes in the head region of *Branchiostoma*, *AmphiHox3*, as a homologue of the vertebrate gene *Hoxb-3*. In the chick, the anterior limit of expression of this gene is between rhombomeres four and five, close to the anterior margin of the hindbrain. In *Branchiostoma*, the homologous gene is expressed between somites four and five within the head region. This indicates that the anterior part of the neural tube occupies a broadly comparable position in cephalochordates and craniates, and hence the sensory and integrative structures in craniates evolved within the region of the cephalochordate "head" rather than in a more anterior position (Peterson 1994). This is further supported by electron microscopy of the cerebral vesicle of larval *Branchiostoma* that shows more vertebratelike features of the sensory structures and their neural circuitry than had been observed in earlier histological studies (Lacalli 1995).

The vertebrate head should not be considered an addition to the existing body of nonvertebrate chordates, as was argued by Gans and Northcutt (1993), but much