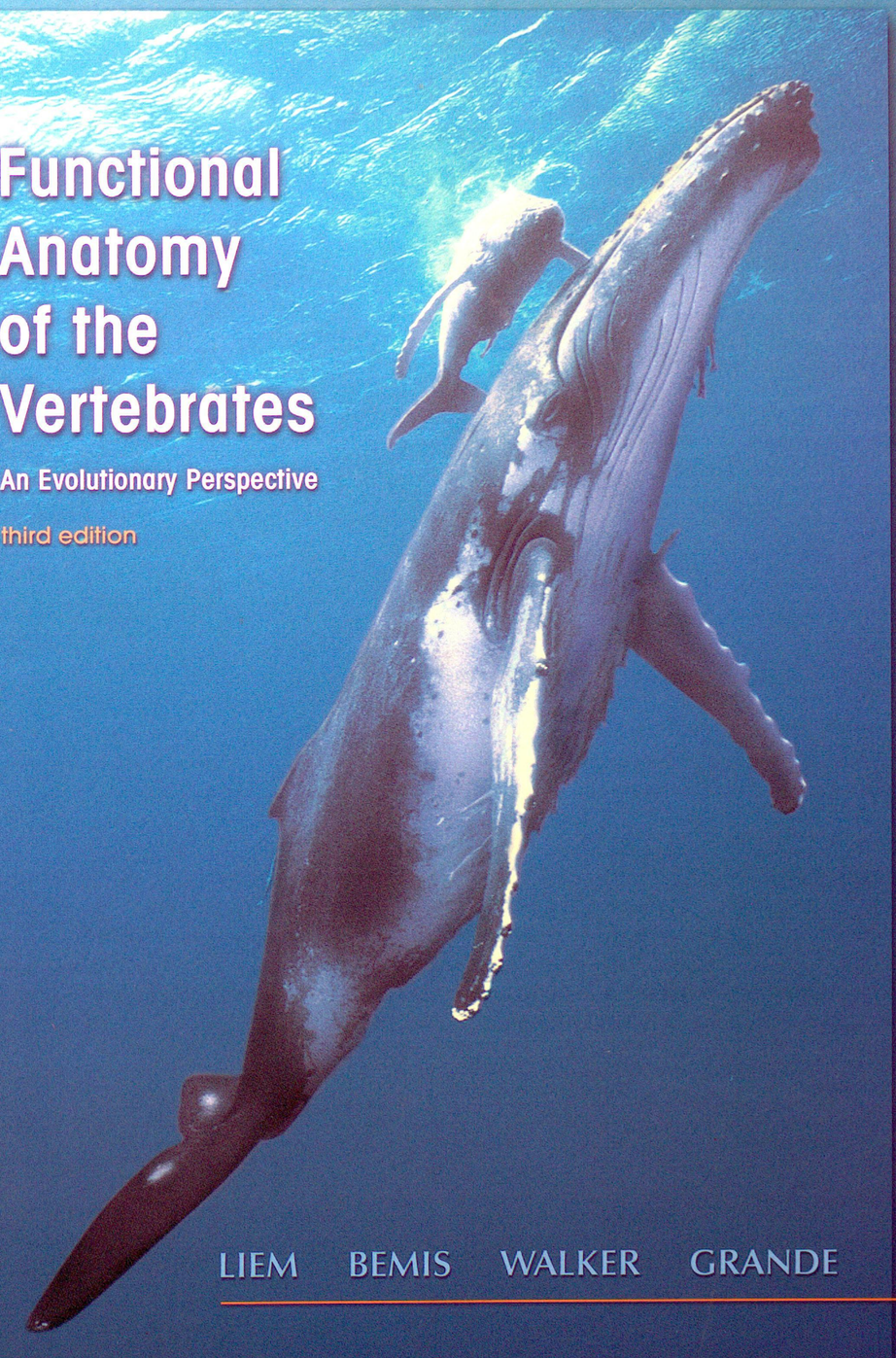
Functional Anatomy of the Vertebrates

An Evolutionary Perspective

third edition



LIEM BEMIS WALKER GRANDE

wall of the pericardial cavity thus consists of the parietal pericardium and parietal pleura, with a thin layer of connective tissue sandwiched between them. This combined wall often is called the **pericardium** or **pericardial sac.**

Many organs lie between the pleural cavities of mammals: the pericardial cavity and heart; the esophagus; major arteries and veins; the phrenic and other nerves; and, in embryonic and young mammals, the thymus. The area between the two pleural cavities that contains these structures is called the **mediastinum.** The mesentery formed where the medial walls of the two pleural cavities meet above and below these structures is the mediastinal septum. Other aspects of mesentery formation and body cavities will be discussed in connection with the gut tube and its derivatives (Chapter 17).

Basic Organization of the Vertebrate Head

Embryogenesis of cranial structures is a major focus in evolutionary morphology because the brain, major sense organs, and many parts of the feeding and respiratory systems are located in the head. Also, the cranial skeleton develops from several different sources, which can be most easily understood from a developmental perspective (see Chapter 7). Elasmobranchs (sharks, skates, and rays) are convenient vertebrates in which to study head development. In contrast to the embryos of most bony fishes, which are typically small and thus strongly curved around their yolk, elasmobranch embryos are large and have a "straight" pharyngeal region that is easy to study (Fig. 4-36). In embryos of amniotes (e.g., the chick) the development of the pharyngeal region has been dramatically altered from the basic plan seen in early vertebrates. No amniotes retain gill slits as an adult, nor do they develop the full complement of aortic arches, nor do they have the lateral line mechanosensory and electrosensory systems that are found in early vertebrates. All three of these features are fundamental to understanding the plesiomorphic structure and organization of the head, thus making elasmobranch embryos the specimens of choice.

Figure 4-37 is a schematic lateral diagram of the head of an idealized shark embryo, based on a famous illustration by an English comparative anatomist and embryologist, Edwin S. Goodrich. Goodrich was interested in detecting the role of segmentation in patterning the structures of the vertebrate head, and his interpretive drawing has influenced generations of anatomists since its publication in the 1930s. The basic arrangement of the cranial nerves is particularly clear from his diagram, and it will be a useful reference throughout your study of vertebrate anatomy.

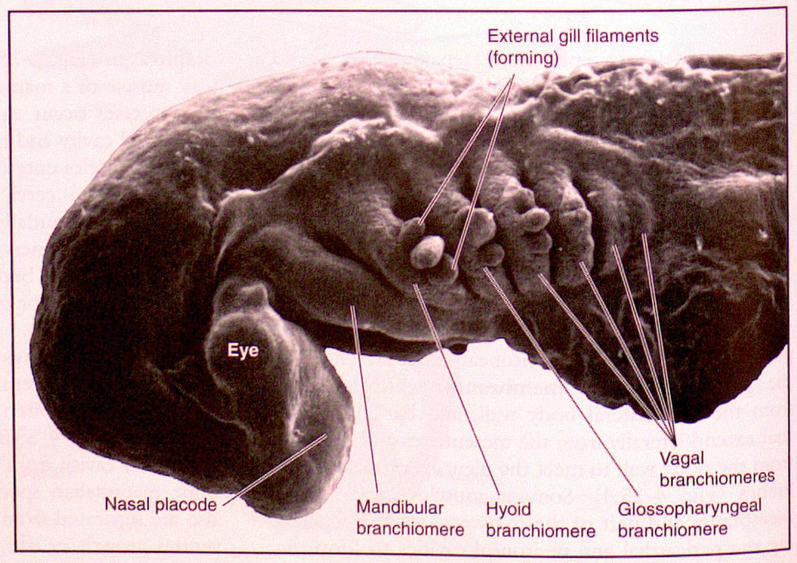


FIGURE 4-36
Scanning electron micrograph showing organization of the gill arches in a skate embryo (*Raja erinacea*). This specimen is at a later stage of development than the one shown in Figure 4-28*F*. Note the well-developed eye; the nearly complete series of branchiomeres and gill slits; and the still small external gill filaments forming on the hyoid, glossopharyngeal, and vagal branchiomeres. The nasal placode is beginning to invaginate to form the nasal pit.

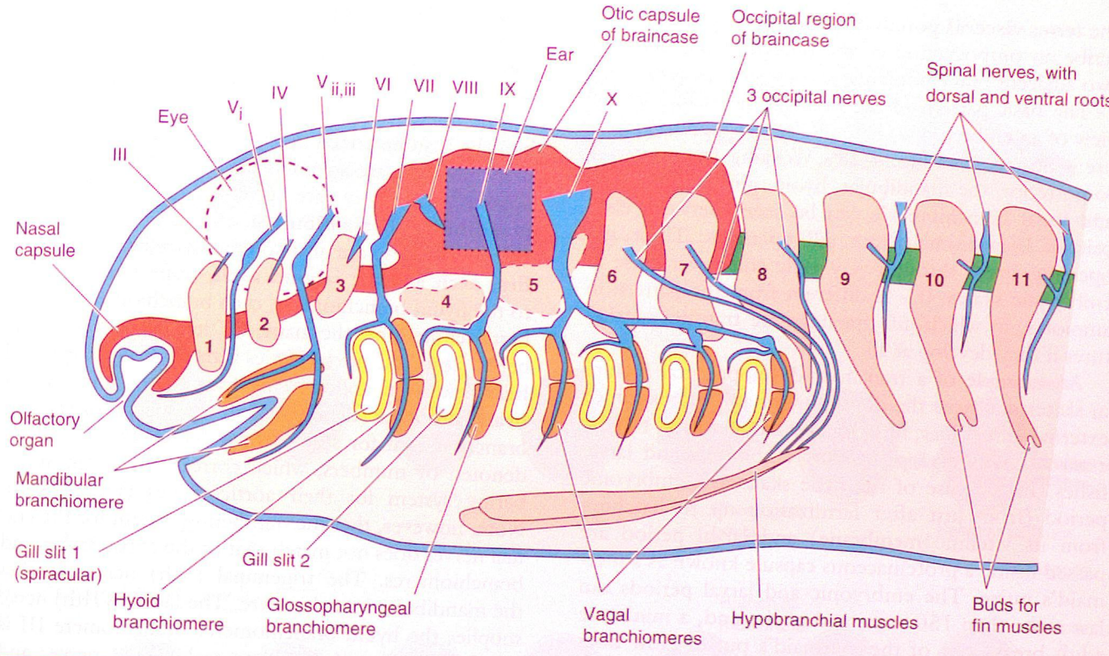


FIGURE 4-37
Semitransparent schematic view of vertebrate head development, based on a shark embryo. The brain is omitted. The diagram illustrates segmentation of the cranial somites and branchiomeres. Somites bear Arabic numerals and are innervated by cranial nerves III, IV, and VI. Branchiomeres located between the gill slits and including the jaws are innervated by cranial nerves V_{ii}, V_{iii}, VII, IX, and X. The braincase and associated nasal and otic sensory capsules are indicated. The myotomes and somatic motor nerves of segments 4 and 5 degenerate and are indicated with dashed lines. *(Based on a figure by Goodrich.)*

Branchiomeres and Pharyngeal Organization

In many textbooks and in the primary literature, the terms "pharyngeal arch," "visceral arch," and "branchial arch" are used inconsistently. Noden (1991) considered the term "branchial arch" least prone to the misinterpretation that all of the cells forming the arches develop from the visceral tube. However, using the word "arch" leaves open the possibility of confusion with the aortic arches or the skeletal arch that forms within a "branchial arch." Also, in adult fishes, "branchial arch" is used to refer to fully differentiated gill arches that carry gill filaments. In the absence of a single, wholly satisfactory term, we consider it best to refer to these embryonic structures collectively as the branchial segments, or **branchiomeres** (Bemis & Grande, 1992). This term branchiomere reflects the obvious segmentation of the gill region while avoiding confusion about either the embryonic sources of their cells or the fully differentiated adult condition. By tradition and because they are good descriptors, we use

the terms **visceral pouch** or **pharyngeal pouch** to describe an outpocketing of the pharynx lying between two adjacent branchiomeres.

The basic pattern of the branchiomeres in a lateral view of an embryo of a skate (*Raja*) is apparent in Figure 4-36 (see also Fig. 4-28). Working from anterior to posterior, the mandibular, hyoid, glossopharyngeal, and vagal branchiomeres can be seen. Between each pair of branchiomeres are gill openings. These gill openings break through very early and never close in embryonic skates; this is different from the pattern in amniotes, in which gill openings are transitory structures if they develop at all.

An example of a transitory developmental feature in skates concerns the development and regression of external gills. Clear, functional reasons exist as to why external gills develop in many embryonic and larval fishes. In the case of the little skate, the embryonic period (from just after fertilization up to hatching from its vitelline membrane) and larval period are passed inside a proteinaceous capsule known as a mermaid's purse. The embryonic and larval periods can last more than 150 days, and at the end, a miniature adult breaks out of the mermaid's purse. How does efficient gas exchange occur within the confines of the mermaid's purse? In Figure 4-36, three small buds are visible on each of the postmandibular branchiomeres. Each of these buds will grow out to form a long, filamentous, capillary loop that serves to exchange respiratory gases. These external gills begin to develop as soon as the heart is sufficiently developed to circulate blood through the aortic arches. In order to have an efficient gas exchange surface, however, it is also necessary to move water over it. Larval skates generate a current by beating the tip of the tail to create a flow of aerated water through small openings in the egg case. This is functionally important because, in such a young larva, the development of the cranial muscles and skeleton is insufficient to allow for the generation of a respiratory current of water by the mechanism used in adults. About halfway through the developmental period, the mouth and relevant cranial skeletal muscular elements are fully functional, and it becomes possible to irrigate the gills by the normal buccal pumping mechanism used by adults (see Chapter 18). From this point on, the external gills regress until they are indistinguishable from the other gill filaments of the gill (i.e., the capillary loops that formed the external gills are retained as part of the regular series of gill filaments in an adult; see Pelster and Bemis, 1992).

A schematic diagram of a horizontal section through the pharynx of an elasmobranch embryo is shown in Figure 4-38. Note in Figure 4-38*A* that each branchiomere contains rami of the cranial nerve associated with that branchiomere,[5] as well as branchiomeric muscle, a skeletal rod, and an aortic arch. In each branchiomere, the lateral surface is covered with ectoderm, and the medial surface is covered with endoderm.

The nomenclature of the branchiomeres in elasmobranchs is summarized in Figure 4-38*B*. The first two branchiomeres are so important in craniofacial development that they are given special names, the **mandibular branchiomere** and the **hyoid branchiomere**; these are also commonly referred to as the **first arch** and the **second arch,** respectively. Caudal to the hyoid branchiomere, each branchiomere may be best denoted by the name of its associated cranial nerve. Thus, the next in series is the **glossopharyngeal branchiomere,** followed by four or even five **vagal branchiomeres** (depending on the species of elasmobranch chosen for study). Branchiomeres also can be denoted by numbers, which correspond to the numbering system for their aortic arches (Fig. 4-38*B*). Note, however, that the numbering system for the cranial nerves does not match that of the aortic arches and branchiomeres. The trigeminal (Vth) nerve supplies the mandibular branchiomere. The facial (VIIth) nerve supplies the hyoid branchiomere. Branchiomere III is supplied by the glossopharyngeal (IXth) nerve, and branchiomeres IV to VII are supplied by rami of the vagal (Xth) nerve (Chapter 13).

In elasmobranchs, **gill slits** develop between each branchiomere and the one anterior to it (Figs. 4-36 and 4-38*B*). Each gill slit or pouch thus has the same number as the branchiomere immediately anterior to it, although these numbers are conventionally written as Arabic numerals instead of Roman numerals. The development of the gill slits is shown in the developmental series of skate embryos illustrated in Figure 4-28. Gill slit 2 is the first to open, followed by gill slit 3, and next by gill slit 1 (which receives the special name of **spiracle**). All but the last gill slit are open in the older skate embryo shown in Figure 4-36. The lack of strict anterior-to-posterior sequence in the opening of the gill slits is undoubtedly related to differences in size and function of the openings in adult elasmobranchs. Before each gill slit "breaks through," we refer to the tissue that occupies the opening as the **branchial membrane.** The pocket on the medial side of each branchial membrane lined with endoderm is known as a **pharyngeal pouch.** Endodermal cells derived from these regions have many different fates, including formation of endocrine glands and organs of the immune system. These fates are traced in Chapter 15.

[5]The post-trematic ramus of the appropriate nerve supplies the skeletal muscles of a branchiomere, so it is usually the largest nerve bundle in a branchiomere; see Figure 13-18*C*.

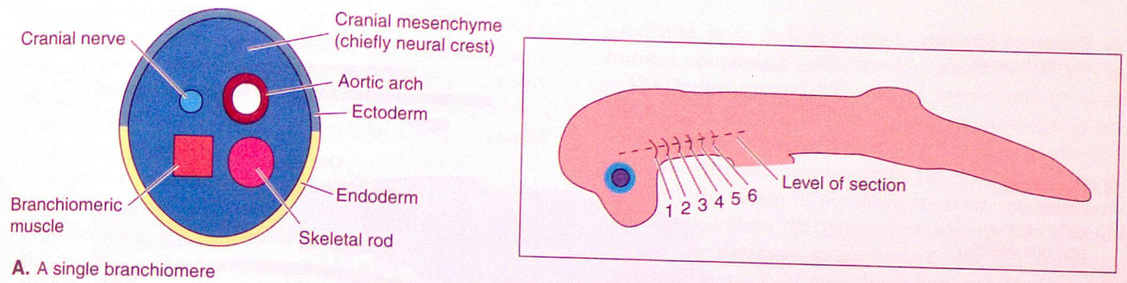
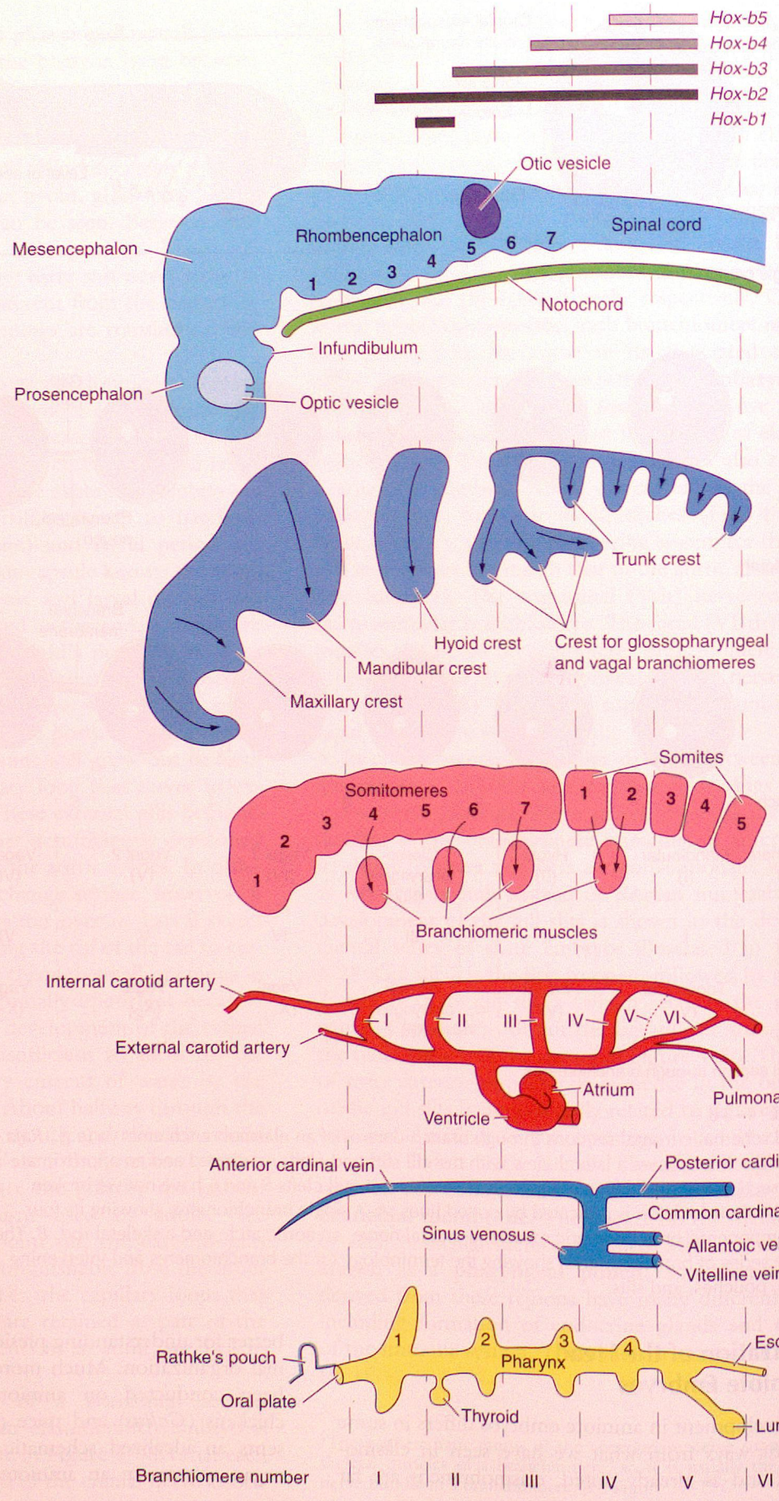


FIGURE 4-38
Idealized schematic frontal sections through branchiomeres of an elasmobranch embryo (e.g., *Raja* or *Squalus*). The inset shows a lateral view with the gill slits and clefts numbered and an approximate plane of section for the schematic figure in *B*. In the inset, gill clefts 5 and 6 have not yet broken through, so their location is indicated by dotted lines. *A*, A single branchiomere, showing its four major components: branchiomeric muscle, a cranial nerve, an aortic arch, and a skeletal rod. *B*, The complete series of branchiomeres, showing the terminology for the branchiomeres and intervening gill clefts, pouches, and slits.

Organization of the Head in Amniote Embryos

Head development in amniote embryos differs in some important ways from what we have seen in elasmobranchs, and as already noted, elasmobranchs are far better for understanding plesiomorphic features of cranial organization. Much more research, however, has been conducted on amniote embryos, particularly chickens (*Gallus*) and mice (*Mus*). Figure 4-39 presents an idealized schematic diagram of the cranial organ systems in an amniote embryo, redrawn from



the elegant synthetic work of Drew Noden (1991). Using gray tic lines to demarcate branchiomeric boundaries, the diagram presents major cranial tissues in registration with each other and with the expression domains of *Hox* genes known to play a role in cranial patterning (Fig. 4-39*A*).

Figure 4-39*B* shows dorsal axial structures, including the neural tube and notochord. The prosencephalon, mesencephalon, and rhombencephalon (the three primary brain regions) are labeled, and the seven rhombomeres in the wall of the hindbrain are numbered. The paired otic and optic vesicles also are shown; these are easily detected reference points when comparing embryonic vertebrates. The anterior tip of the notochord is another important reference point for comparing vertebrate embryos. It also marks the beginning of the "new head" postulated by Northcutt and Gans (1983; see Chapter 2). The **hypophysis** forms immediately anterior to the notochord; its location is demarcated in this diagram by the **infundibulum,** which contributes to formation of the hypophysis (see Fig. 15-4*A*).

Figure 4-39*C* diagrams the cranial neural crest migrating ventrally into the branchiomeres, in movements already introduced in Figure 4-24*B*. The many different fates of these cells were briefly discussed earlier and are summarized in Table 4-2.

Figure 4-39*D* shows the organization of paraxial mesoderm in the head. The anterior portion of the paraxial mesoderm is incompletely divided in amniote embryos. Instead, it consists of a series of seven **somitomeres,** which can be detected using scanning electron microscopy to study carefully dissected embryos. Somitomeres are transient, mesenchymally organized structures, which, unlike true somites, never become "epithelialized" and thus never contain somitocoele cavities. Note that the series of seven somitomeres in amniotes is numbered independently from the somites in the trunk. This convention differs from the standard nomenclature used for elasmobranch embryos, which is shown in Figure 4-37. This is because anterior portions of the paraxial mesoderm of elasmobranchs subdivide into well-developed, epithelially organized somites containing somitocoeles (somites 1–3 in Fig. 4-37). It has proved difficult for researchers to agree on a single alignment and consistent numbering system equating the anterior cranial somites of elasmobranchs with the somitomeres of amniotes. Despite this and the many differences in their organization, cells derived from the paraxial mesoderm are thought to have similar fates in elasmobranchs and amniotes. Much of the paraxial mesoderm forms skeletal muscles of the head, including the extrinsic eye muscles and muscles of the branchiomeres. As determined by Noden (1991) and shown in Figure 4-39*D*, amniote somitomeres 4, 6, and 7, along with several anterior somites, contribute to branchiomeric muscles in branchiomeres I (mandibular), II (hyoid), and III (glossopharyngeal). Somitomeres 1 to 3 and 5 contribute to the extrinsic ocular muscles (see Fig. 13-20).

The major cranial blood vessels are diagrammed in Figure 4-39*E* and *F*. The numbering system for aortic arches used for elasmobranchs (Fig. 4-38*B*) also applies to amniotes, but because amniotes develop fewer vagal branchiomeres, they consequently have fewer aortic arches. Also, the fifth aortic arch never forms in amniotes, and so it is indicated with a dashed line (Fig. 4-39*E*). Major cranial veins, such as the **anterior cardinal vein,** develop by fusions of a plexus of smaller vessels. As in the trunk, cranial blood vessels derive from mesoderm. The precursor cells, known as **angioblasts,** migrate early from their sources and move invasively throughout the head mesenchyme. Angioblasts differentiate into the lining cellular layer of the blood vessels, which is known as **endothelium.** In contrast to veins, arteries tend to develop by branching of existing vessels, a process known as **angiogenesis.** This difference in their mode of formation helps to explain why veins are anatomically more variable than arteries.

The paired pharyngeal pouches are shown in Figure 4-39*G*. As in the scheme shown for elasmobranchs in Figure 4-38, the pharyngeal pouches are numbered with Arabic numerals. The rudiment of the **thyroid**

◀**FIGURE 4-39**
Anatomical relationships among the components of the head in an amniote embryo in lateral view. The diagram is comparable to a stage 14 chick (45 hours, 22 somites). Light gray lines demarcate the approximate boundaries of branchiomeres I, II, III, IV, and V. *A,* Expression domains of genes of the *Hox-b* cluster. *B,* Axial structures including the neural tube and notochord. *C,* Neural crest migrating ventrally into the branchiomeres. *D,* Paraxial mesoderm, incompletely divided into somitomeres anteriorly and completely divided into somites in the trunk; somitomeric contributions to branchiomeres I, II, and III also are indicated. *E,* Heart and aortic arches. *F,* Major veins. *G,* Pharyngeal pouches and Rathke's pouch. Amniote embryos have four paired pharyngeal pouc lined with endoderm; in all gnathostomes, Rathke's pouch forms as a single median diverticulum ectoderm just anterior to the oral plate. *(Modified from Noden.)*

gland originates as a median ventral diverticulum from the floor of the pharynx between the mandibular and hyoid branchiomeres. It extends caudally during later development and ceases to be connected to the pharynx. The developing lung also originates as a median ventral diverticulum; its retained connection to the gut tube will become the trachea. **Rathke's pouch** (Fig. 4-39*G*) is a median dorsal diverticulum of ectoderm that forms just anterior to the oral plate, the region known as the **stomodeum.** As it extends dorsally, Rathke's pouch comes to lie adjacent to the infundibulum, which is a ventral outpocketing of the neural tube (Fig. 4-39*B*). Rathke's pouch and the infundibulum together form the master endocrine gland, the **hypophysis.** The dual embryonic origins of the hypophysis continue to be reflected in the types and mechanisms of hormone production and secretion used by its component parts (see Chapter 15, especially Fig. 15-4).

Hox Genes, Segmentation, and the Evolution of the Vertebrate Body Plan

The connection between development and evolution has drawn the attention of biologists and philosophers for more than a century. The actively growing field of evolutionary developmental biology examines connections between embryology and evolution using tools from molecular biology, phylogenetics, and comparative anatomy. It has long been thought that detailed knowledge of DNA regulatory genes, which are those that control expression of other genes, will prove essential to understanding major features of vertebrate evolution. Perhaps 10% of the genome of a vertebrate consists of DNA regulatory genes, and we still have much to learn about all aspects of the story. To illustrate the type of synthesis that may emerge, we discuss *Hox* genes and their role in the development of the vertebrate body plan.

A **segment** is a set of body parts that is present in a repeated series in an embryo or adult. Segmental organization is fundamental to the vertebrate body plan, and all vertebrates are more or less obviously segmented during their development. Segmentation is most obvious in embryonic stages but often becomes masked in adults, particularly in the cranial region. Nevertheless, we have seen that the head displays several types of interrelated segmentation. Branchiomeres provide clear evidence of segmental organization, as do the rhombomeres of the hindbrain and other components of the head (Fig. 4-39*B*). Cranial neural crest cells migrate ventrally to contribute to the branchiomeres, following the same segmental pattern (Fig. 4-39*C*). The paraxial mesoderm that lies to each side of the developing brain is also segmentally organized, whether as true somites found in elasmobranch embryos (Fig. 4-37) or as the transient somitomeres of amniotes (Fig. 4-39*D*).

The connection between development and evolution can be demonstrated by considering the role of *Hox* genes in regulating the development of such segmented structures.[6] A series of these genes or their homologues is expressed differentially along the length of the body axis; this differential expression pattern helps establish the basic pattern of the segments and instruct the subsequent development of segment-specific features. In this way, *Hox* genes can be thought of as generating unique tags for specific locations in the body.

Hox genes code for **helix-turn-helix transcription factors,** which are DNA binding proteins (Fig. 4-40*A* and *B*). These proteins contain variable regions (green in Fig. 4-40) and highly conserved regions (red in Fig. 4-40). They fold in such a way that their tertiary structure consists of two helical regions separated by a short, variable "turn" region. The very highly conserved sequence of about 60 amino acids, known as the **homeodomain,** forms a recognition helix that can be presented to the major groove in the double-helical DNA molecule (Fig. 4-40*B*).

The portion of a *Hox* gene that codes for the homeodomain portion of the transcription factor is called a **homeobox.** Many families of genes contain homeoboxes. Thus, not all genes containing homeobox sequences are *Hox* genes, but these are the best known genes in this class. Wherever homeobox sequences occur in the genome, they code for remarkably similar amino acid sequences. These sequences also are preserved across remarkable phylogenetic gaps: 59 of the 60 amino acid residues in some homeodomains of vertebrates and fruit flies are identical. Such evolutionary conservation is an outstanding example of the tight link between structure and function at the molecular level because, if the homeodomain portion of the transcription factor does not fit precisely into the major groove of the DNA double helix, then it cannot function. The highly conserved homeodomain region, however, is just one part of the transcription factor. The remaining regions of the protein can be of variable length and differ from one Hox protein to the next. It is the regions outside the homeodomain that allow the transcription factor to bind with other specific factors in order to recognize specific genes along a DNA strand (Fig. 4-40*C–E*). By means of their variable regions, different Hox proteins can regulate expression of different genes.

Proteins made by a particular *Hox* gene are found inside cells in a restricted and specific set of segments of the body. The places where a particular gene is expressed are known as that gene's **expression domain.** By regulating the expression of other genes, *Hox* genes determine the features that are characteristic of each body segment. This is the result of unique expression domains or unique combinations of overlapping expression domains. Perturbation experiments, known as "knockout" experiments, involve the deletion or inactivation of a particular gene, usually by mutation. A *Hox* gene that has been knocked out may result in a specific segmentation defect or defects; defects do not necessarily result because other genes can sometimes

[6]By convention, the word *Hox* is italicized to indicate a DNA sequence or gene; when not italicized, the word Hox indicates an amino acid sequence or protein.

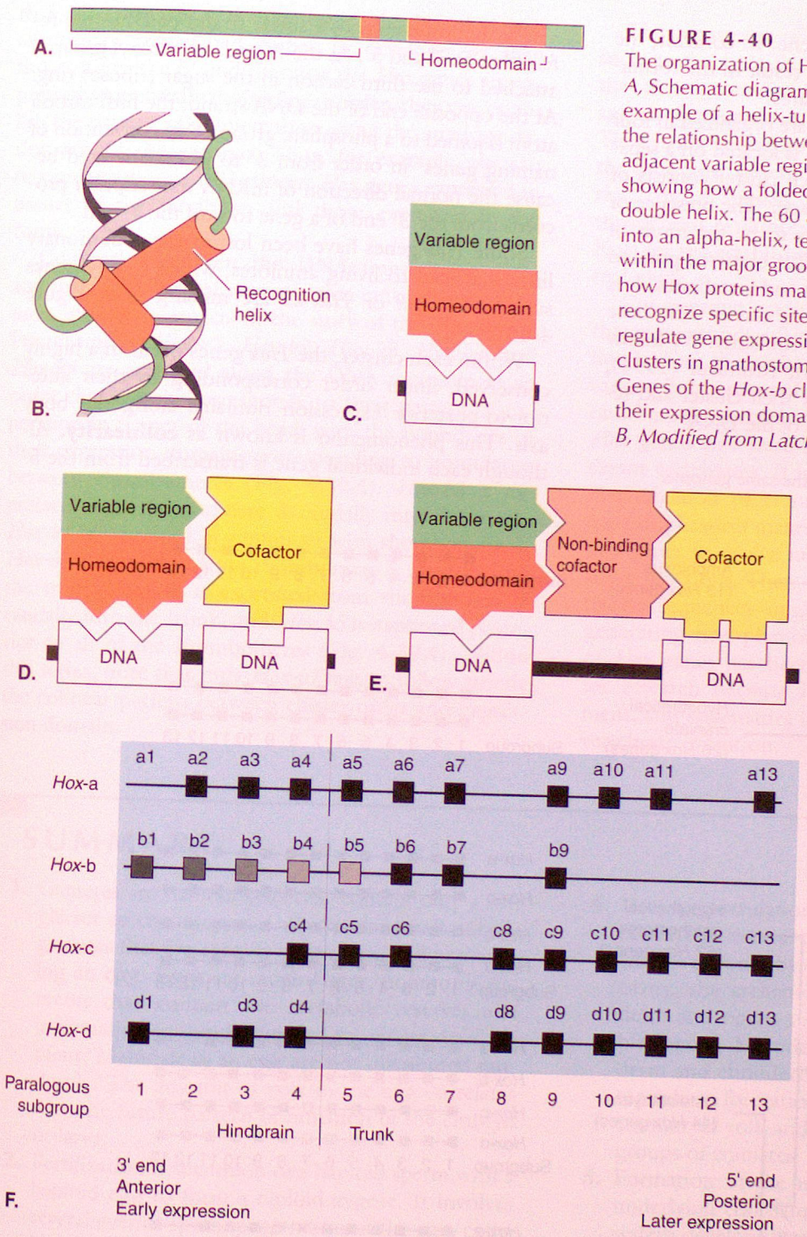


FIGURE 4-40
The organization of Hox proteins and *Hox* genes. *A,* Schematic diagram of a Hox protein, which is an example of a helix-turn-helix transcription factor, showing the relationship between highly conserved region (*red*) and adjacent variable regions (*green*). *B,* Schematic diagram showing how a folded Hox protein interacts with a DNA double helix. The 60 amino acid homeodomain folds up into an alpha-helix, termed a recognition helix, that fits within the major groove of the DNA. *C–E,* Models showing how Hox proteins may interact with other factors to recognize specific sites within the genome in order to regulate gene expression. *F,* The structure of *Hox* gene clusters in gnathostomes, based on the mouse (*Mus*). Genes of the *Hox-b* cluster are shaded to correspond with their expression domains indicated in Figure 4-39*A*. *(A and B, Modified from Latchman; D, modified from Krumlauf.)*

take over the role of the missing gene. In contrast, the insertion of an extra *Hox* gene can result in the formation of additional segmental structures.

The *Hox* genes of gnathostomes are organized in four clusters, a through d, each of which is located on a separate chromosome (Fig. 4-40*F*). Each cluster consists of as many as 13 **paralogous subgroups.**[7] The presence of these paralogous subgroups appears to be the result of tandem duplications of *Hox* genes that occurred prior to the common ancestry of arthropods and vertebrates. It is possible to align the *Hox* genes of one cluster with those of other clusters based on sequence similarity. We follow the nomenclature of Scott (1992), Krumlauf (1994), and others in naming the genes by their cluster and sequence order from the 3′ to 5′ end of the DNA.

[7]A paralogue is a copy of a gene within the same genome.

The opposite ends of a single strand of DNA are referred to as 3′ and 5′. At the 3′ end, a hydroxyl group is attached to the third carbon in the sugar (ribose) ring. At the opposite end of the DNA strand, the fifth carbon atom is joined to a phosphate group. This convention of naming genes in order from 3′ to 5′ ends is used because the normal direction of mRNA transcription proceeds from the 3′ end of a gene toward the 5′ end.

Some *Hox* genes have been lost in the evolutionary lines that lead to living amniotes, which is why genes such as *Hox-a8* or *Hox-d2* are missing from Figure 4-40*F*.

Within each cluster, the *Hox* genes occur in a highly conserved, linear order corresponding to their anterior-to-posterior expression domains along the body axis. This phenomenon is known as **colinearity.** Although each individual gene is transcribed from the 5′ to 3′ direction, those that lie toward the 3′ end of each cluster are transcribed earlier in development than those nearer the 5′ end. Because the *Hox* genes are expressed sequentially in this linear order, they can establish the pattern of segmentation along the anteroposterior axis of the embryo. Thus, for example, we can recognize a boundary between *Hox* genes expressed in tissues of the hindbrain and those expressed in the trunk.

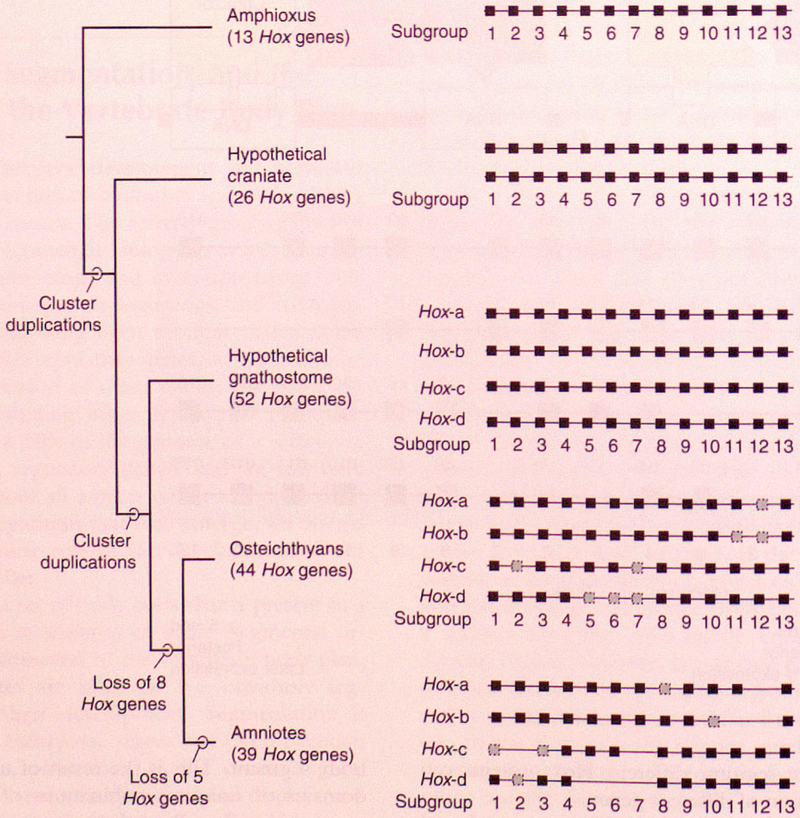


FIGURE 4-41
Phylogenetic tree of chordates showing position of *Hox* gene cluster duplications by Holland et al. (1994), and the subsequent losses of individual *Hox* genes proposed by Meyer (1998). Based on analyses of *Hox* genes in amphioxus, hagfish, lampreys, basal osteichthyans, and amniotes. Genes shown with dashed lines have been lost. *(Modified from Holland et al. and Meyer.)*

Colinearity between the DNA transcription level and the appearance of segmentation ranks as one of the most intriguing aspects of the story of the *Hox* genes. For example, *Hox-b1*, *Hox-b2*, *Hox-b3*, *Hox-b4*, and *Hox-b5* are arranged along the DNA molecule in an order that closely corresponds to their pattern of expression in tissues of the head, with the boundaries of their expression domains corresponding to boundaries between rhombomeres (Fig. 4-39*A*). *Hox-b2* is expressed from rhombomere 3 caudally into the trunk, *Hox-b1* is expressed in alignment with rhombomere 4, *Hox-b3* is expressed from rhombomere 5 caudally into the trunk, *Hox-b4* is expressed from rhombomere 7 caudally into the trunk, and *Hox-b5* is expressed posterior to all of the rhombomeres (Fig. 4-39*A*). Within this series, note that only *Hox-b1* fails to follow strictly the colinear pattern between cluster order and expression domain.

The occurrence of homologues of *Hox* genes in taxa such as the fruit fly, *Drosophila*, supports the notion that these genes first evolved at least 600 million years ago in flatworms or other early bilateral metazoans. Their truly remarkable constancy suggests that once the molecular system for determining the anteroposterior axis of animals was established, it was retained throughout evolutionary history and has served as the basis for the establishment of diverse body plans in animal phyla.

Comparative studies on *Hox* gene clusters suggest that two rounds of gene duplication occurred in the line leading to craniates, with the first round of duplications between amphioxus and craniates, and the second between hagfishes and gnathostomes (Fig. 4-41). *Hox* genes also were lost in some lineages leading to extant vertebrates. It is tempting to attribute the great diversification of craniates to these duplications, for gene duplication makes it possible for copies of particular genes to evolve rapidly without impairing any existing functions. Then, at a later time, some altered duplicate sequences might be "recaptured" for use in generating new phenotypes. The comparative analysis of *Hox* genes has become an extremely exciting area for research because it combines genetics, development, and systematics in the search for explanations in vertebrate evolution.

SUMMARY

1. Gametes are haploid cells that contain only a single set of chromosomes. Sperm are small, motile gametes that are capable of reaching and penetrating an egg. Eggs are much larger, nonmotile gametes that contain the metabolic reserves and information molecules needed to initiate development. Materials in an egg are not distributed randomly. The amount of yolk in the egg correlates with the future pattern of nutrition of the embryo or larva.
2. Fertilization is the union of a haploid sperm with a haploid egg to form a diploid zygote. It involves several events: sperm penetration of the egg, combination of male and female nuclear material, and activation of the egg.
3. During cleavage, the single-celled zygote is converted to a multicellular embryo called a blastula, but no growth occurs. Because the materials in the egg were not distributed evenly, the cells (blastomeres) in different parts of the blastula contain different enzymes, mRNAs, and other components. As a result, the blastomeres differ in their presumptive fates.
4. During gastrulation, the single-layered blastula is converted into a two-layered gastrula. The gastrula is covered by ectoderm and has a simple gut cavity, the archenteron, which is lined by endoderm and opens to the surface posteriorly at the blastopore. Mesoderm spreads between the ectoderm and endoderm. Patterns of gastrulation and mesoderm formation are greatly influenced by the amount of yolk and vary considerably in different groups of craniates.
5. Formation of the neural tube is induced by the underlying chordamesoderm. The central nervous system develops from the neural tube.
6. In addition to the neural tube, vertebrates have two other neurogenic tissues: the neural crest and neurogenic placodes.
7. Ectodermal neural crest cells separate during the formation of the neural tube and spread throughout the embryo. They give rise to many structures (i.e., branchial skeleton, other cranial bones, pigment cells, many peripheral neurons, parts of teeth, and bony scales) and also help regulate development and the emergence of the