

The notochord develops early in vertebrates and at first consists of tightly packed cells that resemble a pile of coins. The cells soon enlarge and become vacuolated. A fully developed notochord consists of enlarged notochordal cells and a relatively complex *notochordal sheath* (fig. 6.1). The superficial cells of the notochord have their nuclei aligned

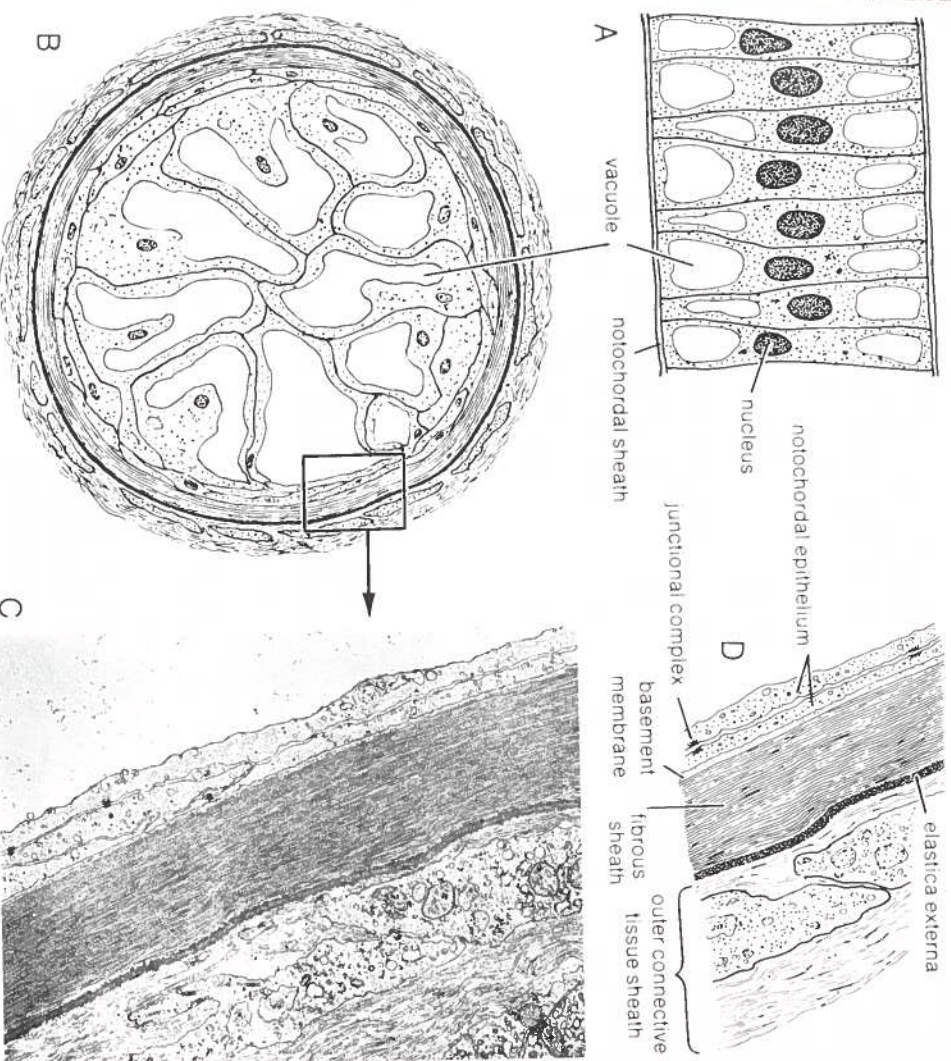


Fig. 6.1. The notochord of a generalized vertebrate. *A*, sagittal section of a developmental stage, at which the cells are layered like a pile of coins. *B*, cross section through the notochord of a tadpole of the African clawed frog, *Xenopus laevis*. *C*, electron micrograph illustrating detail of a portion of the notochordal sheath region, courtesy Richard M. Cloney, University of Washington. *D*, diagrammatic representation of portion of *C*.

near the surface and are often termed the *notochordal epithelium*. All notochordal cells are joined by junctional complexes characteristic of epithelia. The first layer of the sheath is the *basement membrane* of the notochordal epithelium. Surrounding this is a very thick *fibrous sheath* composed of collagen fibers. The next layer is the much thinner *elastica externa*, composed of elastin fibers. Finally, an *outer connective tissue sheath* of alternating strata of flattened fibroblasts and collagen fibers

## 6 The Endoskeleton: The Comparative Anatomy of the Vertebral Column and Ribs David B. Wake

### A. General Considerations on the Endoskeleton

The endoskeleton is the internal supporting system of hardened material characteristic of vertebrates. The endoskeleton of vertebrates consists of cartilage, bone, or mixtures of these two types of tissue, and is mainly mesodermal in origin. The parts of the endoskeleton of vertebrates are: the *skull*, in the head; the *visceral skeleton*, composed of *gill arches* supporting the gills, and their derivatives; the *vertebral column*, occupying the median dorsal region; the *ribs*, projecting from the vertebrae one pair to each vertebra primitively; the *sternum*, occupying the median ventral region of the anterior part of the trunk; the *pectoral girdle*, supporting the anterior paired appendages; the *pelvic girdle*, supporting the anterior paired appendages; and the *skeleton* of the *appendages*. The four parts first named constitute the *axial skeleton*, and other parts constitute the *appendicular skeleton*.

### 1. The Endoskeleton and Its Parts

#### 2. The Notochord

The *notochord*, or *chorda dorsalis*, is a stiffened rod extending longitudinally in the middorsal region of the chordate body, just beneath the central nervous system. It probably originated as a support for an elongated body of an organism that swam by lateral undulations. In larval vertebrates it is a resilient rod that restores the body to its elongated resting position after flexion. It is formed embryologically from the roof of the archenteron or its equivalent. In tunicates the notochord forms a supporting rod for the "tadpole" larva. In those species that metamorphose, the tail and the notochord are resorbed. This occurs quickly, either through the action of a contractile tail epidermis, in some species, or by the contraction of notochordal cells themselves in other species. In the latter case, the notochord ruptures anteriorly and its contents enter the body cavity of the trunk. In *Branchiostoma* the notochord constitutes the axial support of the body. Recently, early reports that the *Branchiostoma* notochord contains muscle fibers have been confirmed, and it appears that a unique muscular mechanism permits the organ to vary its stiffness. Embryos of all vertebrates have a notochord, and in them it extends anteriorly to the level of the hypophysis. In *Branchiostoma*, however, it extends virtually to the anterior tip of the body. In most vertebrates the vertebral column replaces the notochord as the main axial support during later stages of development. The vertebral column forms around the notochord and gradually squeezes it out of existence or reduces it to remnants that are often restricted to the areas between vertebrae. In some groups the notochord may persist throughout life, however, and may play an important functional role in the adult.

joins the notochord to surrounding tissues. In some accounts the fibrous sheath alone is termed the notochordal sheath, and in early treatments the entire sheath is said to be composed of an *elastica interna* and an *elastica externa*. These features, based on light microscopy, are not easily reconciled with the above account based on electron microscopy. Recently an *elastica interna*, lying between the basement membrane and the fibrous sheath, has been found in the distal part of the tail of frog tadpoles.

### 3. The Skeleto- genous Regions

The endoskeleton develops from mesenchyme. The mesenchyme for the vertebral column and ribs comes chiefly from the sclerotomes that are formed by the breakdown of the medial sides of the epimeres (somites) into mesenchyme; but contributions from other mesodermal sources also occur. The mesenchyme accumulates around the notochord and neural tube and in certain other *skeletogenous regions*. The arrangement of the latter is largely dependent on the disposition of the myotomes. The myotomes or muscle segments, which are those portions of the epimeres remaining, grow down between the skin and the digestive tract to form the muscular layer of the body wall. Each myotome is separated from adjacent ones by a transverse partition of mesenchyme, the *myoseptum* or *myocomma*. Each myotome (except in cyclostomes) is further divided into a dorsal (*epaxial*) and a ventral (*hypaxial*) half by a horizontal partition, the *horizontal skeletogenous septum*, which extends from the notochord to the level of the lateral line on the sides of the body. The mesenchyme surrounding the notochord (*perichordal mesenchyme*) and neural tube continues to the median dorsal line as the *dorsal skeletogenous septum*, and similarly from the notochord to the median ventral line (in the tail) as the ventral skeletogenous septum. In the trunk region the *ventral skeletogenous septum* is naturally split into two *ventrolateral* septa which become the outer wall of the coelom (fig. 6.2). The horizontal, dorsal, and ventral septa are continuous longitudinal septa, extending the length of the body. As their name implies, the skeletogenous septa are regions of skeleton formation. At the inter-

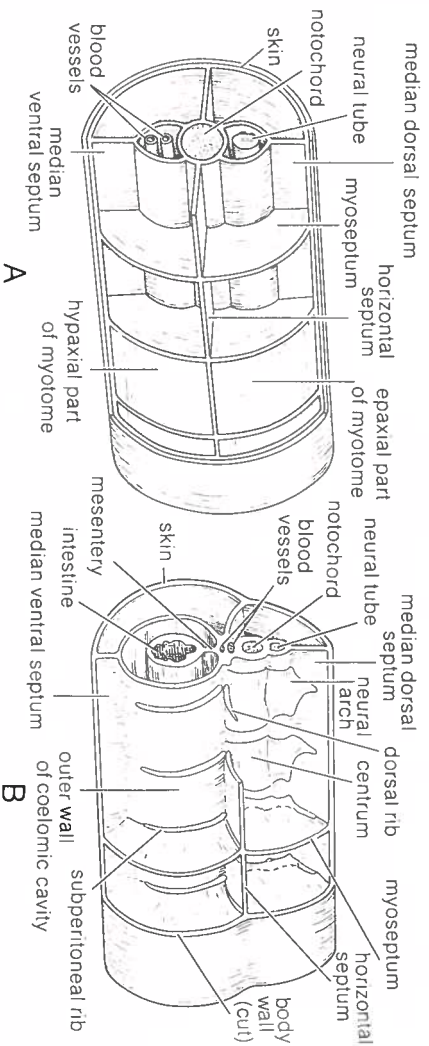


Fig. 6.2. Diagrams to show the skeleton-forming septa in *A*, the tail region, and *B*, the trunk region of a generalized vertebrate.

*section of every myoseptum with the dorsal, ventral, and horizontal septa and with the perichordal mesenchyme, a vertebra arises. As the myosepta are segmentally repeated, because of the primary segmentation of the myotomes, it follows that the vertebrae are also segmentally repeated and that the vertebrae alternate with the myotomes.*

### B. Anatomy and Embryonic Origin of Vertebrae and Ribs

#### 1. Parts of a Typical Vertebra

The axis of the vertebrate skeleton is the *vertebral column* or backbone, composed of a longitudinal series of bones, the *vertebrae*. A typical vertebra consists of a central cylindrical mass, the *body* or *centrum*, that surrounds and replaces or incorporates the notochord, a dorsal *neural arch* inclosing the spinal cord, and a ventral *hemal arch*, inclosing blood vessels (fig. 6.3*A*). Neural and hemal arches are commonly prolonged dorsally and ventrally, respectively, into *neural* and *hemal* spines. In the trunk region the hemal arch is typically missing. A vertebra also com-

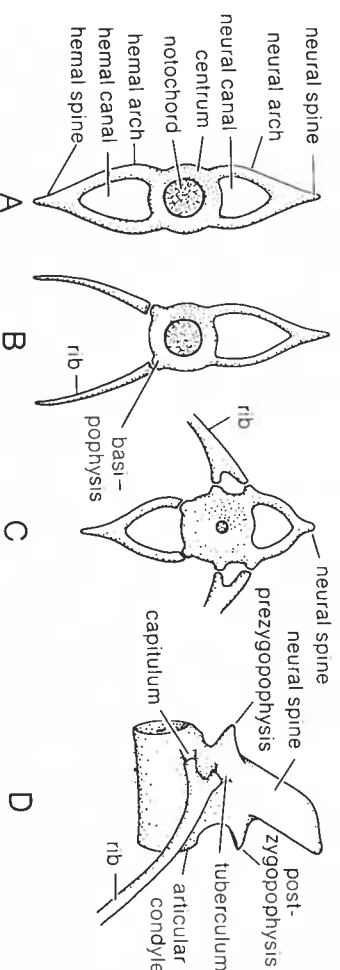


Fig. 6.3. Diagrams of generalized vertebrae. *A*, cross section of tail vertebra of a teleost fish. *B*, cross section of trunk vertebra of the same, showing opening of the hemal arch to form the basapophyses. *C*, cross section of trunk vertebra of a terrestrial vertebrate, showing attachments of ribs. *D*, lateral view of a trunk vertebra of a salamander, showing characteristic processes and attachment of ribs.

monly has a variety of projecting processes, termed *apophyses*, serving for articulation with adjoining vertebrae or with ribs or for muscle attachment. The most common apophyses are:

- Zygapophyses*, articulations between successive vertebrae; they are divisible into *prezygapophyses*, anterior projections, and *postzygapophyses*, posterior projections, of the basal region of the neural arch (fig. 6.3).
- Basapophyses*, also called hemapophyses or basal stumps, are a pair of ventral projections of the centrum, which in some cases represent the remains of the hemal arch and may serve for rib attachment (fig. 6.3).
- Diapophyses*, lateral projections of the vertebra for the attachment of the upper head of two-headed ribs (fig. 6.3).
- Parapophyses*, lateral projections of the vertebra for the attachment of the lower head of two-headed ribs (fig. 6.3).
- Pleurapophyses*, lateral projections representing the rib attachments of the vertebra plus the fused rib.
- Hypapophyses*, midventral projections from the centrum.

The expression *transverse process* for any lateral projections of vertebrae is useful, although it must be understood that it has no exact morphological meaning. Often transverse processes and pleurapophyses are synonymous, but diapophyses alone may also be termed transverse processes. In some groups the diapophysis and parapophysis may fuse to form a *synapophysis*; this composite structure is also often called a transverse process. On the tail vertebrae, transverse processes are formed that cannot be positively identified according to the more specific terminology above.

2. Shapes of Centra

The vertebral column is formed and functions as an axial support by the end-to-end placement of the centra of the vertebrae. The shape of the ends of the centra is thus important in the mechanics of the vertebral column (fig. 6.4); generally applied terms include:

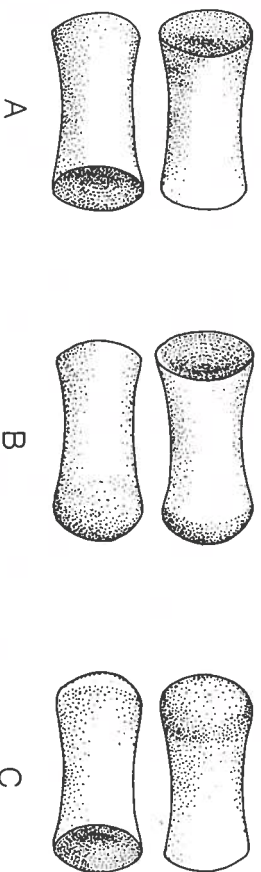


Fig. 6.4. Diagrams of the anterior (top) and posterior (bottom) ends of the centra of vertebrates, to show the varied articular shapes. A, amphicoelous. B, procoelous. C, opisthocoelous. D, heterocoelous. E, amphiplatyan.

- a) *Amphicoelous*, both ends concave.
- b) *Procoelous*, anterior end concave, posterior end convex.
- c) *Opisthocoelous*, anterior end convex, posterior end concave.
- d) *Heterocoelous*, both ends shaped like the seat of a saddle placed transversely at one end and vertically at the other.
- e) *Amphiplatyan*, both ends flat.

These terms are strictly anatomical and relate solely to the bone, without reference to the extremely important fibrous and cartilaginous parts that play important functional roles in joints. Other shapes occur infrequently.

Between the ends of the centra are found the remains of the notochord, intervertebral disks of fibrocartilage or, in some groups, masses of hyaline and fibrous intervertebral cartilage.

3. Development of the Vertebrae

The vertebrae arise from cells that migrate medially, surround the notochord and neural tube, and spread along the skeletogenous septa as mesenchyme. These cells produce a more-or-less continuous *perichordal tube*, whose thickness varies along its length and from group to group. Typically the perichordal tube bears enlargements, *perichordal rings*, that surround the notochord near the midpoint of each segment. Cartilage usually appears in the mesenchyme of the skeletogenous regions. This cartilage may persist, often stiffened by mineralization, or may undergo partial or complete ossification. First appearance of the cartilaginous masses is in intersegmental locations, in the intermyotomal recesses that lie vertically along the notochord and neural tube (fig. 6.5). In

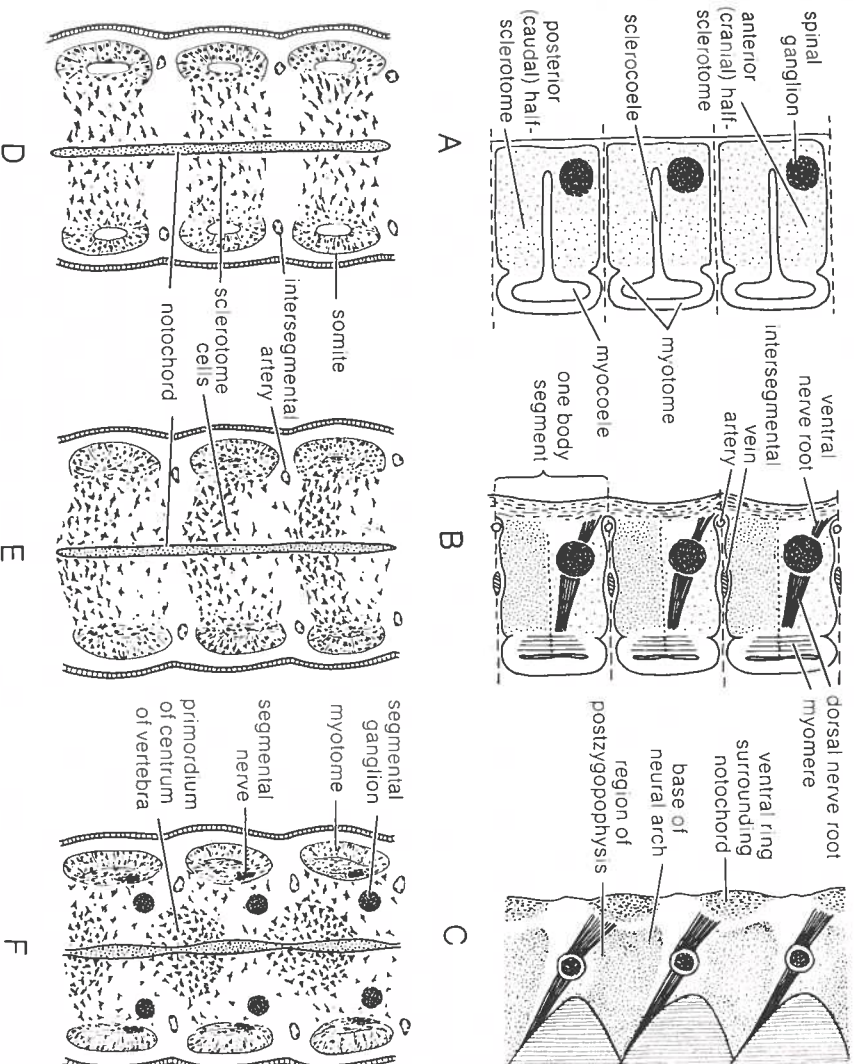


Fig. 6.5. Development of the vertebral column. A, highly diagrammatic frontal section through right half of the prevertebral stage, to show the parts of the somites and their relation to the notochord and ganglia. B, later stage, to show that the cranial half-sclerotome (sclerotomite) is denser than the caudal half-sclerotome. C, start of skeletogenesis, to show that the base of the neural arch forms in close proximity to the skeletogenous ring surrounding the notochord that will become the centrum. D, developmental stage similar to B, but not so diagrammatic. E, developmental stage similar to C, but not so diagrammatic. F, developmental stage similar to A, but not so diagrammatic. A, B, C, modified after Remane (1936). D, E, F, modified after Patten 1958 (*Foundations of embryology*. New York: McGraw-Hill).

most vertebrates direct ossification of the sclerotomal mesenchyme also occurs, and the vertebra is compounded of parts performed in cartilage and parts that ossify directly. The vertebral column thus forms around the notochord, which is inclosed inside the centra, where it persists in the more primitive vertebrates. In more advanced vertebrates the notochord is gradually reduced and replaced by the developing centra and persists only between vertebrae as highly modified remnants.

The vertebrae are derived from somites, but in order to function they have an out-of-phase metamerism, relative to the musculature derived from the myotomes. In other words, muscles must run from vertebra to vertebra in order to bend the vertebral column. To accomplish this, development of the major parts of the vertebrae takes place at myotomal borders. This is intersegmental or transsegmental development. Cells from a given sclerotome concentrate at sites in the vicinity of segmental borders. Areas of low cell concentration in the anterior part of a segment (generally termed the *cranial sclerotomie*, fig. 6.5B,E) are thought by many workers to contribute to the posterior parts of one vertebra, and the dense column of cells in the posterior part of each segment (termed the *caudal sclerotomie*) contributes in a major way to the anterior and central parts of the next vertebra. Each vertebra therefore seemingly incorporates parts of two adjacent sclerotomes. In annelids the sclerotome is cell-rich, and distinct sclerotomal units, divided into distinct cranial and caudal sclerotomites, are evident. The caudal sclerotomite is especially evident as a prominent condensation. These two cell masses are usually said to undergo a reorganization to form the vertebrae, but recently this has been questioned, for it seems that very little, if anything, is contributed by the cranial sclerotomite (fig. 6.5C,F). In fishes and most amphibians the sclerotome is generally scanty and is not clearly divided into parts. Yet the vertebrae form at myotomal borders, and cells from adjacent sclerotomes might contribute to the adult vertebra even though this has not been directly observed. In all vertebrates the original sclerotomal segmentation pattern of the early embryo is lost with the formation of the continuous perichordal tube. The adult vertebrae form from the perichordal tube in transsegmental positions; a resegmentation can be said to occur if one focuses on the fact that segmental muscles run between vertebrae. However, Baur (1969) and Verbout (1974) argued that vertebrae form at the caudal end of each segment and that no reorganization is required. According to this view, vertebrae arise from the beginning at their definitive sites, and there is no shifting of segment parts or regrouping of segment halves. Most illustrations in textbooks are in error in showing blocks of tissue that separate, migrate, and regroup to form definitive vertebrae, but it is still too early to go so far as to deny that vertebrae are formed from components of adjacent segments. This remains an area of controversy.

#### 4. Vertebral Components

In primitive fishes the vertebral column consists of separate parts that arise independently. These parts are attached to each other in various ways, but individual vertebrae may be difficult to identify. In the past, numerous attempts have been made to explain the development and evolution of the vertebrae of more derived groups in terms of fusions, en-

largements, reductions, and elimination of these separate elements. Notable among these attempts are those of Gadow, whose work had great influence for many years. His views have been increasingly criticized, and recently his ideas concerning tetrapods have specifically been challenged. Components are recognizable in all vertebrates, but their homologies are not at all clear, except in a most general way. These basic components are:

##### a. Arch Components

Definite paired cartilages (called *arcualia* by Gadow) appear in primitive fishes and give rise to adult vertebral parts. Typically there are four pairs to each vertebral unit (fig. 6.6). The two largest pairs of elements arise from tissue of the caudal part of each sclerotome. The dorsal pair (called "*basidorsals*" by Gadow) produce the neural arch, and in the tail region the ventral pair ("*basiventrals*") give rise to the hemal arch. Together these arches become the cranial and dominant parts of the adult vertebra. Usually their basal portions rest against the notochordal sheath. Other cartilages may form above the neural arch and below the hemal arch, and these contribute to the formation of neural and hemal spines. Although originally separate entities, the paired cartilaginous elements grow around the neural tube and caudal blood vessels and fuse to form the arches of the adult vertebrae. In addition to these dominant elements, intercalary elements may be present between successive dorsal and ventral arches (fig. 6.6). In some instances both dorsal and ventral intercalary cartilages (termed "*interdorsals*" and "*interventrals*" by Gadow) are present in the posterior parts of the vertebra. These seem to originate from the cranial parts of sclerotomes. In some groups (elas-

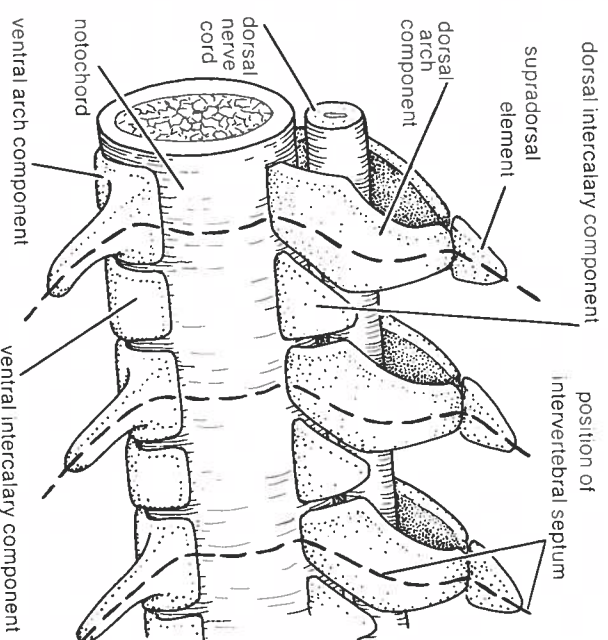


Fig. 6.6. Generalized vertebral column of a primitive fish, viewed laterally, to show major components.

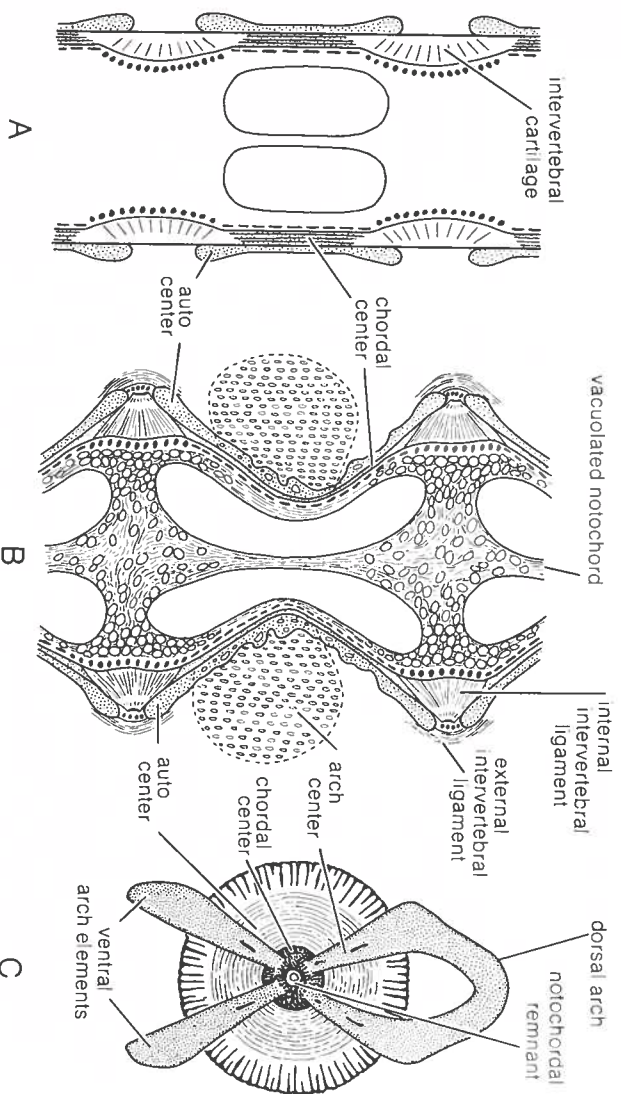


Fig. 6.7. Components of fish centra. *A*, early developmental stage of centrum, showing major components (after Francois 1966), frontal section. *B*, later developmental condition (after Francois 1966). *C*, cross section of later developmental stage, showing interpretation of three developmental centers.

observed in many fish groups. The notochordal sheath itself first undergoes differentiation, with vertebral parts forming *chordal centers* of mineralized, lacunar tissue. Intervertebral parts thicken but remain unmineralized and give rise to parts of the intervertebral ligaments. The *auto center* forms from mesenchyme surrounding the notochord. This tissue produces a series of bony lamellae that are continuous with those covering the cartilaginous arch elements. As a result of this process, the

mobranchs) the intercalaries are rather large and may form complete arches. The dorsal intercalary arch may persist as a large, complete arch in the adult, and it often bears the foramen for the dorsal root of the spinal nerves. Ventral intercalaries are less well developed. Dorsal and ventral arches may fuse with the intercalaries in various patterns in different groups of primitive fishes. In teleosts, cartilaginous intercalaries seem to be absent, and neural and hemal arches are the sole arch components. Some attempts have been made to identify embryonic mesenchymatous masses between neural arch rudiments in several teleosts with dorsal intercalaries. These masses give rise to the interarch articulations (zygapophyses), and their homology with dorsal intercalaries is dubious. Only two pairs of arches are ever present in tetrapods, and these are directly comparable with the neural and hemal arches of fishes.

#### b. Centrum Components

Three major kinds of developmental "centers" may contribute to the body, or centrum, of the adult fish vertebra (fig. 6.7). All three may be

bases of these cartilages are incorporated into the centrum, forming *arch centers*. The three different centers in *Salmo* have three distinct kinds of ossification patterns. The chordal centers are formed of compact acellular bone, or osteoid tissue. The auto centers are the result of perichondrial, membranous ossification. The arch centers, late in development, may undergo endochondral ossification. In other species they may remain cartilaginous.

The most primitive fishes (agnathans, sturgeons) lack distinctive centers and may be termed *acentrous*. Sturgeons have well-developed cartilaginous arches, but dorsal and ventral arches fail to join, except anteriorly, and no perichondrial tissue develops.

Various conditions prevail in chondrichthyans. Many have centra with the same components as in *Salmo*, but some lack auto centers. Some holocephalans also lack arch centers, but these do have chordal centers.

*Polypterus* has vertebrae similar to those of *Salmo* in terms of centrum components, and holosteans have predominant arch centers. Many teleosts are like *Salmo*, in which the auto centers are responsible for most of the centrum, but with large arch centers as well. In various groups of derived teleosts the arch centers may be very reduced or even absent. The chordal centers may be of minor significance and become reduced in size and importance as the large auto center thickens, squeezing the notochord.

Centrum components are essentially absent in lungfishes and *Latimeria*, in which the notochord is essentially unconstricted. What little skeletal tissue is found in the "centrum" of these groups seems to be formed from perichordal mesenchyme, but the cartilaginous arch elements are expanded where they come into contact with the notochord.

All tetrapods have centra that form almost exclusively from perichordal mesenchyme. In most groups the centrum is first laid down in cartilage, which is later replaced by bone, but in some amphibians most of the bony centrum forms directly from mesenchyme. This material, whether preformed in cartilage or not, can be considered an auto center. The bases of the neural and hemal arches may contribute to the adult centrum in amphibians (arch centers).

## 5. The Ribs

Each vertebra is theoretically provided with a pair of *ribs*, which articulate to various projections of the centrum and extend out into the body wall. Ribs serve to strengthen the body wall and provide muscle attachments. The ribs, like other parts of the axial skeleton, arise in the skeletal togenous septa. There are two kinds of ribs, both of which are situated in the myosepta and hence are segmental in arrangement. One type is formed at the intersection of each myoseptum with the horizontal skeletal togenous septum. Since the horizontal septum divides the myotomes into dorsal and ventral halves, such ribs lie between the muscles and hence are called *intermuscular ribs*, also *dorsal* or *upper ribs*. The second type of rib arises at the points of intersection of the myosepta with the ventral skeletal togenous septa or its derivatives. In the trunk region the ventral septum is split into two lateral septa because of the intervention of the coelom and its contents on the ventral side of the body. The second

type of rib appears at the points of intersection of the myosepta with these ventrolateral septa. They typically lie just outside the coelomic lining between the coelomic wall and the muscle layer (fig. 6.8). They are therefore called *subperitoneal* ribs, also *ventral*, *lower*, or *pleural* ribs. Both kinds of ribs may occur simultaneously on a vertebra, and in fact some fishes may have additional ribs of the category of dorsal ribs. The ventral or pleural ribs are generally thought to be the older phylogenetically.

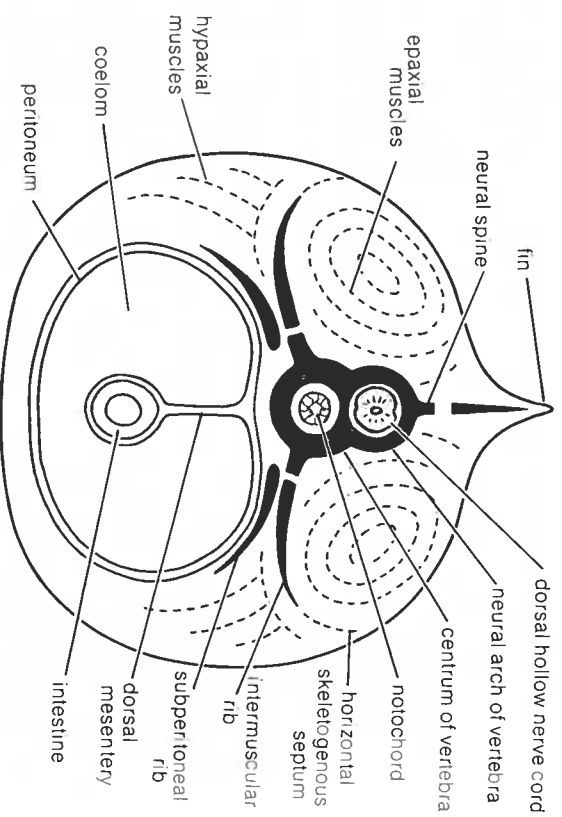


Fig. 6.8. Diagrammatic cross section through the trunk of a vertebrate to show the relation of the ribs to the skeletogenous region, and the positions of the two kinds of ribs.

### C. Vertebral Columns of Some Archaic Fishes

Vertebral columns of the most primitive living vertebrates are rather poorly developed and consist of separate pieces, often cartilaginous in structure. Because of the cartilaginous structure of primitive vertebrate and the poor fossil record for living relicts (e.g., lampreys, primitive actinopterygians), it is difficult to reconstruct the early history of the vertebral column. From all available evidence it appears that elements of the dorsal arch were the first to appear, followed by ventral arches and finally by centra. Thus the early vertebrae, formed of arch parts only, are called *acentrous*.

#### 1. Vertebral Column of Cyclostomes

The notochord of lampreys and hagfishes is well developed and has a thick sheath. Vertebral elements of hagfishes are erratically developed and irregular in shape from segment to segment. The tiny dorsal elements lie against the nerve cord, and they are largely restricted in distribution to the tail region. In lampreys, three kinds of dorsal elements are present, and we will call them A, B, and C for purposes of orientation. In the anterior part of the trunk A and B are fused together and are penetrated by a foramen serving the ventral root of the spinal nerve. Between these relatively large cartilages are very tiny cartilaginous pieces, C (fig. 6.9). By the midtrunk region A and B are separated and C is

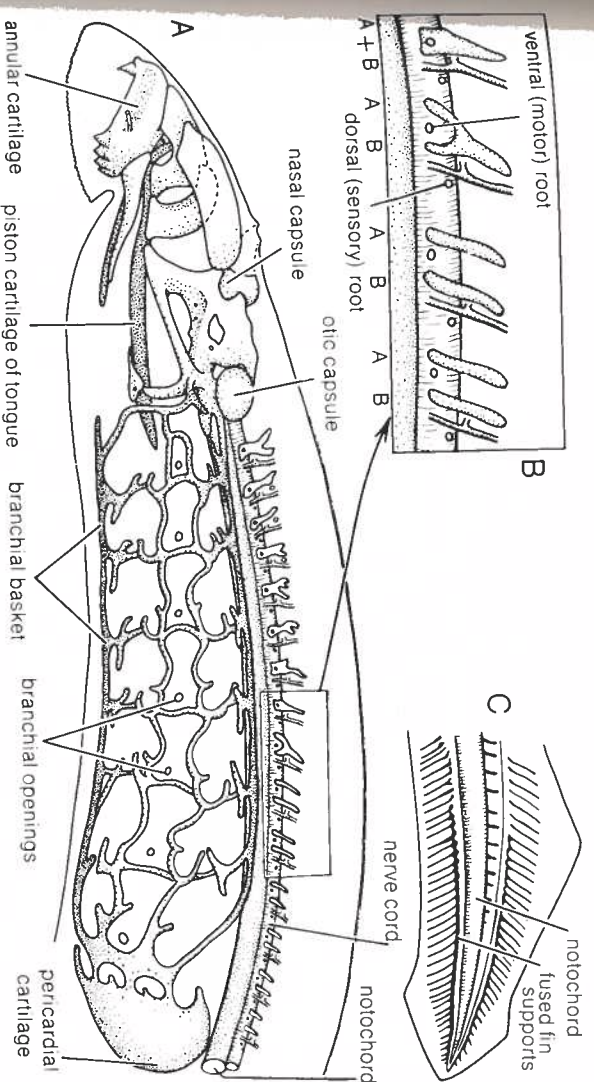


Fig. 6.9. The skeleton of a lamprey. A, the anterior end, to show the small, poorly developed vertebral elements lying along the large notochord (after Jollie 1962 [*Chordate morphology*, New York: Reinhold]). B, enlargement of the transitional region to show separation of vertebral elements (after Remane 1936). C, the tail region to show fusion of bases of fin supports around notochord (after Remane 1936).

absent. Thus in this region there are also two pairs of dorsal cartilages per segment. Posteriorly the development of A and B is erratic, and they may be fused to each other, separated, or one or the other may be absent. Ventral arch elements have been reported in the tails of lampreys, but it is unclear whether these are more than the expanded bases of the cartilaginous fin supports. The fin supports tend to fuse basally in the tail region, and more or less continuous cartilaginous structures extend for some distance in the tail region (fig. 6.9C). Homologies of the vertebral elements in cyclostomes with those of fishes are unclear.

#### 2. Vertebral Column of the Sturgeon

The vertebrae of sturgeons and related fishes are composed of separate cartilaginous arches that rest on the large notochord (fig. 6.10). There is no centrum. The unconstricted notochord traverses the center of the vertebral column and is covered dorsally and ventrally by cartilage pieces, leaving its lateral exposure uncovered by skeletal elements. Large dorsal arch elements develop in the myosepta and unite above the nerve cord to form a neural arch. The arch is topped by a separate unpaired element, the *neural spine*. Dorsal intercalaries develop in each segment, anterior to the dorsal arch. The intercalaries are variable in number, size, and shape, and there is often more than one pair per segment. Ventral arches and intercalaries have positions corresponding to those of their dorsal counterparts. The ventral arches bear large processes for articulation with ribs, and a small cartilaginous bridge joins them anteriorly. Posteriorly in the trunk and tail the arches join to form the hemal arch.

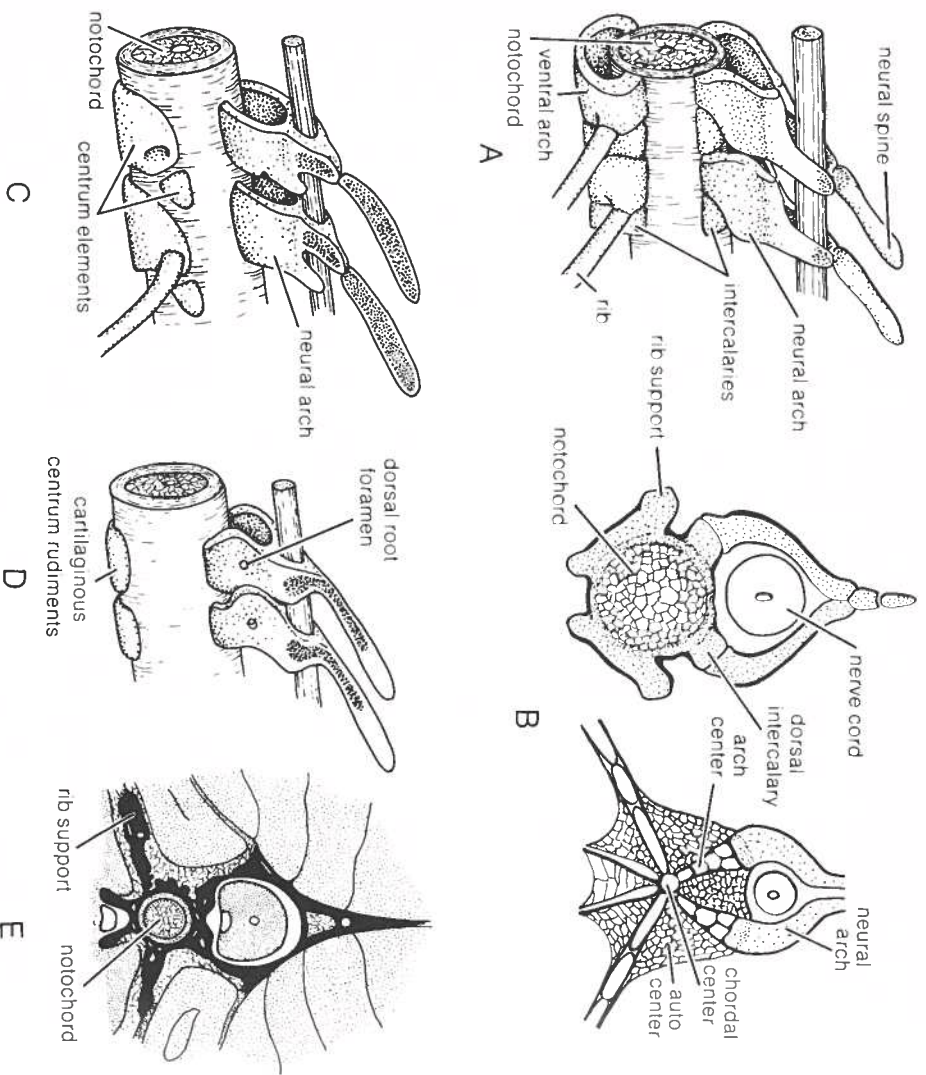


Fig. 6.10. The vertebrae of some archaic fishes. *A*, lateral view of the posterior trunk vertebrae of a sturgeon. *B*, cross sections of developmental (left) and adult (right) trunk vertebrae of *Amia* (after Schaeffer 1967). *C*, lateral view of the trunk vertebrae of a lungfish *Neoceratodus*. *D*, lateral view of the trunk vertebrae of *Latimeria*. *E*, cross section of a trunk vertebra of a larval *Protoperus* (after Budgett 1900 [Trans. Zool. Soc. Lond., vol. 16]).

### 3. Vertebral Column of *Polypterus*

The fish *Polypterus* has well-developed bony vertebrae formed of dorsal and ventral arches and centra (fig. 6.10). The neural spine, which forms as an independent element, is also joined with these elements to produce the adult vertebra. Ventral arch elements are primarily in the form of ventrolateral processes of the centrum, which serve for rib articulation. Hemal arches are present in the tail region.

### 4. Vertebral Column of *Amia*

The centrum of *Amia* is well developed. Arch components play a large role in its formation (Schaeffer 1967). In the abdominal region dorsal intercalaries become incorporated into the adult centrum and form the bases for the neural arch (fig. 6.10). Ventral intercalaries are absent, and the ventral arches themselves are incorporated into the adult centrum, from which they protrude as rib supports (laterally) and small ventral processes. In the caudal region ventral as well as dorsal inter-

calaries are present in development, and their presence seems associated with the curious arrangement of adult vertebrae in the tail. Centra bearing neural and hemal arches alternate with ones devoid of arches, so that there are two centra to each tail segment. Developmentally the dorsal and ventral intercalaries of a given segment are incorporated into the more anterior centrum (called the *precentrum*), while the bases of the neural and hemal arches are embedded in the more posterior centrum (called the *postcentrum*). This arrangement is probably functionally important in increasing the flexibility of the tail region relative to the rest of the vertebral column.

### 5. Vertebral Column of Lungfish

Lungfishes have a large, unstricted notochord with a thick fibrous sheath (fig. 6.10). Ossified neural arches rest on parts of the sheath that may also be ossified. Some lungfishes may have thin, ring-like centra, but they are generally absent. Rib supports also rest on the fibrous sheath, possibly on local areas of ossification. Hemal arches are present in the tail region, and small dorsal intercalaries are present in some species.

### 6. Vertebral Column of *Latimeria*

The large, unstricted notochord is surrounded by a thick fibrous sheath and a thinner elastic one (fig. 6.10). No centra are present. The ribs and neural arches rest on the sheath, as do the hemal arches in the tail region. The only vertebral parts that ossify are parts of the neural arches and spines.

### D. Vertebral Column of the Dogfish

#### 1. Cross Section of the Tail

Obtain a cross section through the tail of the dogfish and study the cut surface, being sure that the section passes through the junction between vertebrae and not through the center of a vertebra. (When the section passes through the center of the vertebra, areas of calcification in the form of rings or rays will be seen.) The center of the section contains the vertebra, composed of clear, relatively soft cartilage. Between the vertebra and the skin is a thick layer of voluntary muscles, composed of a number of leaves, the myotomes or muscle segments, separated from each other by plates of connective tissue, the myosepta. The myotomes appear in whorls because they zigzag in form like those of *Branchiostoma*, and hence a number will be cut across in any cross section. The myotomes are somewhat indistinctly divided into dorsal and ventral portions by a connective tissue partition, the horizontal skeletal septum, which extends from the centrum of the vertebra to the skin, where it meets the lateral line. The muscles above the septum are the dorsal or *epaxial* muscles; those below it, the ventral or *hypaxial* muscles.

The vertebra itself consists of a central circular concave portion, the *centrum* or *body*; dorsal to this is the *neural arch*, which encloses a cavity, the *neural canal*, in which the soft, white spinal cord is situated. Ventral to the centrum is the *hemal arch*, which encloses a cavity, the *hemal canal*, containing the *caudal artery* and *vein*. The neural arch terminates in a point, the *neural spine*, and the hemal arch similarly terminates in the *hemal spine*. Observe the connective tissue partitions that extend from the neural spine to the median dorsal line and

from the hemal spine to the median ventral line. These are *dorsal* and *ventral skeletogenous septa*; and they, together with the horizontal skeletogenous septum already mentioned, mark the chief sites of skeleton formation.

## 2. Sagittal Section of the Tail

Obtain or make a median sagittal section through the tail of a dogfish. Identify the centra in the section. Each consists of two somewhat triangular pieces, apparently separate, the rounded apexes of the triangles directed toward each other, the whole shaped somewhat like an hourglass. The two ends of the centra are concave, so that diamond-shaped spaces are present between successive centra. These spaces are filled with a soft, gelatinous material, the notochord, which also fills the canal that runs through the center of the centrum. Hence the notochord is constricted by the centra but expands to nearly its embryonic size in the space left between the concave ends of adjacent centra (fig. 6.11). The centra of elasmobranchs are thus biconcave or *amphicoel-*

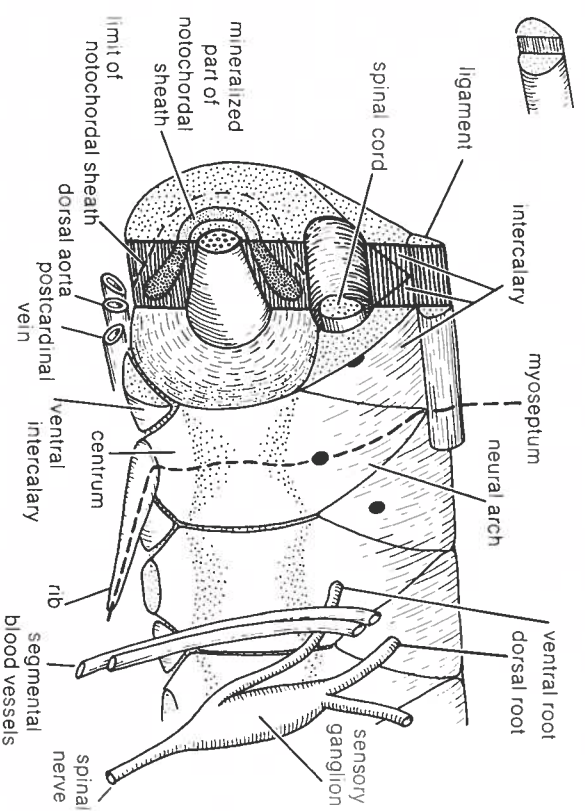


Fig. 6.11. Vertebral column of a shark, partially cut away to show details of the complex notochord-centrum relationship. After Jollie 1962 (*Chordate morphology*. New York: Reinhold).

*ous*. Above each centrum identify the neural arch, arching over the neural canal. Between successive neural arches, and lying therefore dorsal to the diamond-shaped spaces between the centra, observe an extra arch, inverted, however, with apex enclosing the neural canal. This is the *intercalary arch*. Below the centrum is the hemal canal, its sides formed by the hemal arches, rectangular in section.

## 3. Cross Section of the Trunk Region

In a cross section of the anterior part of the trunk region of a dogfish identify the following parts. The muscle segments are arranged as in the tail region, their division into dorsal and ventral masses being well

marked by the horizontal skeletogenous septum. The dorsal or *epaxial* muscles above the septum are thick masses, but the ventral or *hypaxial* muscles below the septum form a thin layer enclosing a large cavity, the *body cavity* or *coelom*, lined by a smooth membrane, the *pleuroperitoneum*. The coelom incloses the viscera, some of which will be observed to be suspended by a delicate membrane, the *dorsal mesenterly*, from the median dorsal line of the coelomic wall. The vertebra consists of centrum and neural arch, similar in appearance to those of tail vertebrae; but the hemal arch is absent. It may be represented by a pair of small cartilages at the sides of the ventral part of the centrum. These are the *basapophyses* or *basal stumps*, the apparent homologues of the hemal arch. Examine the horizontal skeletogenous septum carefully and find within it, by picking away the muscles if necessary, a slender cartilage on each side, articulating with the basapophyses. These cartilages are the ribs.

## 4. Preserved Skeleton

The vertebral column may be conveniently divided into trunk and tail, with all tail vertebrae having hemal arches. The vertebra are composed of several distinct parts (fig. 6.11). The main part of each vertebra consists of the centrum and the neural arch. The centrum in the trunk region bears a pair of ventrolateral ridges, the basapophyses. The neural arch narrows dorsally to an apex. The spaces between adjacent arches are filled with large intercalary arches which are long dorsally and have a ventral apex on either side of the neural canal. Each neural arch is penetrated by a foramen for the passage of the ventral root of the spinal nerve. The dorsal roots pass through more dorsally located foramina in the intercalaries. Ventrally, small intercalaries lie at the junctions of centra.

Short ribs articulate with the basapophyses. These extend into the myosepta at the level of the horizontal skeletogenous septum.

## E. Vertebral Column of Teleosts

### 1. The Tail Vertebrae

Examine a separate, dried tail vertebra of a bony fish. Note that the bony vertebra is very much harder and more opaque than the cartilaginous dogfish vertebrae. Identify the parts already seen in the dogfish vertebrae: the biconcave or amphicoelous centrum, bearing a minute canal in its center for the notochord; the neural arch, terminating in a very long, sharp neural spine; the hemal arch, terminating in a hemal spine (fig. 6.12D). The neural canal enclosed within the neural arch is generally smaller than the hemal canal, enclosed by the hemal arch. The spines are directed posteriorly. In some fish there are two neural spines to each vertebra, an anterior and a posterior; the second one probably corresponds to the intercalary arch of the dogfish.

### 2. The Trunk Vertebrae

Obtain a separate dried trunk vertebra of a bony fish. Identify, as before, the centrum and the neural arch and neural spine. A small ossification, called a supradorsal, may be present along a ligament that extends through the dorsal part of the neural arch. The hemal arch and spine are missing (fig. 6.12). A pair of projections at the sides of the base of the centrum each bear a long slender rib.



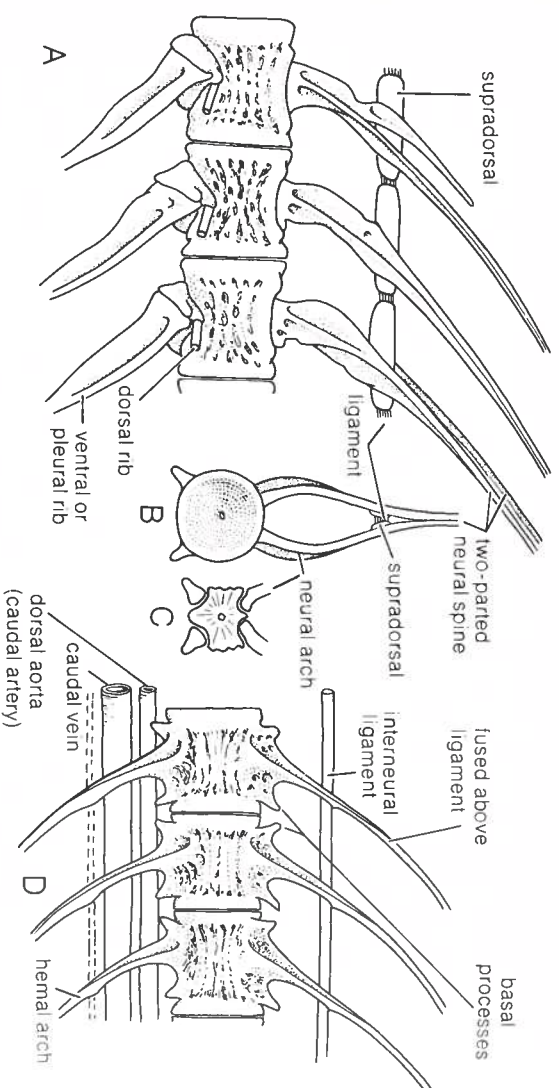


Fig. 6.12. Vertebral structure in a salmon (after Jollie 1962 [*Chordate morphology*. New York: Reinhold]). A, lateral view of anterior trunk vertebrae. B, anterior view of a trunk vertebra. C, cross section through middle of centrum. D, lateral view of tail vertebrae.

### 3. Section Through the Trunk of a Bony Fish

Identify the parts already described for a similar cross section of the dogfish. Note the muscle segments, the centrum and neural arch and spine of the vertebra, and the coelom with its lining. Find the ribs, situated just outside the coelomic lining; this location, together with the facts of their development, shows that the ribs of teleosts are pleural (subperitoneal) ribs, like those of elasmobranchs.

### 4. Further Study of Ribs

Some fishes have two (or more) pairs of ribs on each vertebra. Examples are *Polypterus* (p. 00) and many teleosts, including members of the salmon, herring, and pike families. Examine the skeleton of *Polypterus* and note two pairs of ribs attached to each vertebra. The dorsal ribs are articulated to projecting processes of the centrum; the lower or pleural ribs are loosely attached to the ventral surface of the centrum. In the intact fish the dorsal ribs are situated in the horizontal septum, the pleural ribs along the peritoneum. Vertebrae of fishes like the salmon may also be examined, or sections through the trunk of such fishes. Note the pleural ribs; also the dorsal ribs in the horizontal septum. Additional ribs may also be present dorsal to these, articulated with the centrum or neural arch and extending out into the myosepta between myotomes. Teleost ribs approximately equivalent to dorsal ribs may be formed at any level of the myosepta.

### 5. The Vertebral Column as a Whole

Study a mounted skeleton of a bony fish, noting its complete ossification. Observe that the vertebral column is formed by the end-to-end placement of the centra, held together in life by ligaments and muscles. The ends of the centra of fish in general are amphicoelous, and the con-

siderable space left by the concavities of the ends is occupied in life by the remains of the notochord. The vertebral column is divisible into *trunk* and *tail* regions. In the former are the long slender ribs; in the tail region, hemal arches replace the ribs. Observe the transition between trunk and tail regions, noting gradual elongation of the basapophyses and reduction of the ribs toward the posterior end of the trunk. At the beginning of the tail region the reduced ribs finally vanish, and the elongated basapophyses fuse to form the hemal arches. This transition in teleost fishes is considered evidence that the pleural ribs are equivalent to the hemal arches.

Note that the neural arches of successive vertebrae together enclose a continuous neural canal that contains the spinal cord. Similarly, the hemal arches of the tail vertebrae inclose a continuous hemal canal containing blood vessels.

### F. Endoskeletal Fin Supports of Fishes

#### 1. Median Fins

The fins of fishes are supported by dermal rays that articulate with endoskeletal supports, the *pterygiophores*, more or less concealed in the animal. Here only the unpaired fins will be considered, since the paired fins are treated in the next chapter.

On skeletons of elasmobranch and teleost fish note the endoskeletal supports between the dermal rays of the median fins and the neural and hemal spines of the vertebrae. In elasmobranchs these pterygiophores compose one or more rows of cartilaginous pieces or rods, which are usually larger and fewer in number next to the vertebrae. In teleosts a row of slender bony rods, sometimes flattened, is articulated with the vertebral spines at one end and the dermal fin rays at the other. There may be one or more such pterygiophores to each vertebral spine (fig. 6.13). These pterygiophores seem to be cutoff portions of the vertebral spines.

#### 2. Tail Fin

The dermal rays of the tail fin of fishes are articulated directly to the arches of the vertebrae. Much attention has been paid to the form of this

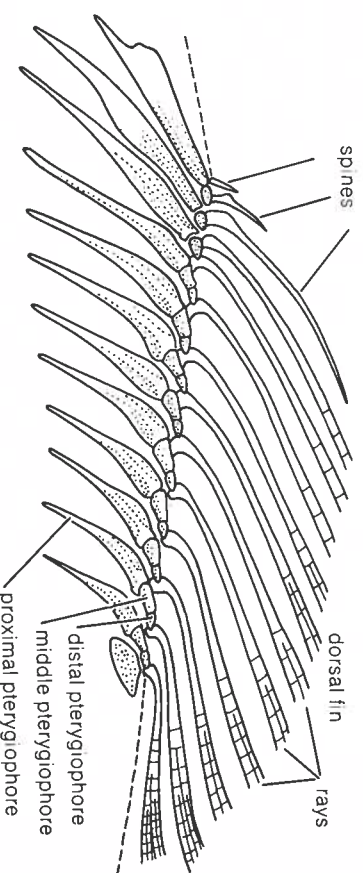


Fig. 6.13. Skeletal supports of dorsal fin of a teleost fish, to show spines, rays, and their supports. Dotted line indicates limit of body of fish. After Jollie 1962 (*Chordate morphology*. New York: Reinhold).

terminal part of the vertebral column, and several types are recognized (fig. 6.14):

*a. Protoconical Tail*

Hypothetical primitive type, perfectly bilaterally symmetrical with fin developed equally above and below the straight vertebral (or notochordal) axis; found in cyclostomes and passed through in the development of teleosts.

*b. Heterocercal Tail*

Asymmetrical with vertebral axis or notochord bent upward in the tail so that the external fin is larger below than above the axis; characteristic of elasmobranchs and most other lower fishes. Examine the skeleton of an elasmobranch and note asymmetrical tail fin with vertebral column turning upward in it. Observe larger fin expanse below than above the column, and particularly note that the anterior part of the lower fin is expanded into a lobe, which probably represents an originally separate fin now fused to the true tail fin. Note how dermal fin rays articulate to the neural and hemal arches of the vertebrae and that the hemal arches are larger and more expanded than the neural ones. A reversed heterocercal (hypocercal) tail, with vertebral column bending downward and lobe on the upper side, is characteristic of certain ostracoderms.

*c. Diphyccercal Tail*

Secondarily symmetrical tails, derived by modification from the heterocercal type; seen in present Dipnoi and coelocanth *Crossopterygii*. They resemble the protoconical type, but intermediate fossil forms show their derivation from the heterocercal condition.

*d. Homocercal Tail*

Externally more or less symmetrical but internally like a shortened heterocercal type; found in all higher fishes and derived during embryology from the heterocercal type. Examine the tail of a skeleton of any bony fish. Note upturned end of the vertebral column with last centrum (probably consisting of several fused centra), forming an elongated urostyle that turns sharply upward. The hemal arches accompanying this upturned part of the vertebral column are enlarged and flattened, forming the *hypural* bones, and a few corresponding enlarged neural arches, or *epural* bones, may be present. It is seen that the tail fin is formed largely or wholly of the ventral part of the fin of the heterocercal tail with a great reduction or loss of the dorsal part. This ventral fin has become secondarily bilaterally symmetrical, so that the homocercal tail appears symmetrical externally. Various modifications of the homocercal tail are found, and two extremes, the cod (a simplified tail) and the tuna (highly adapted for speed) are illustrated in figure 6.14.

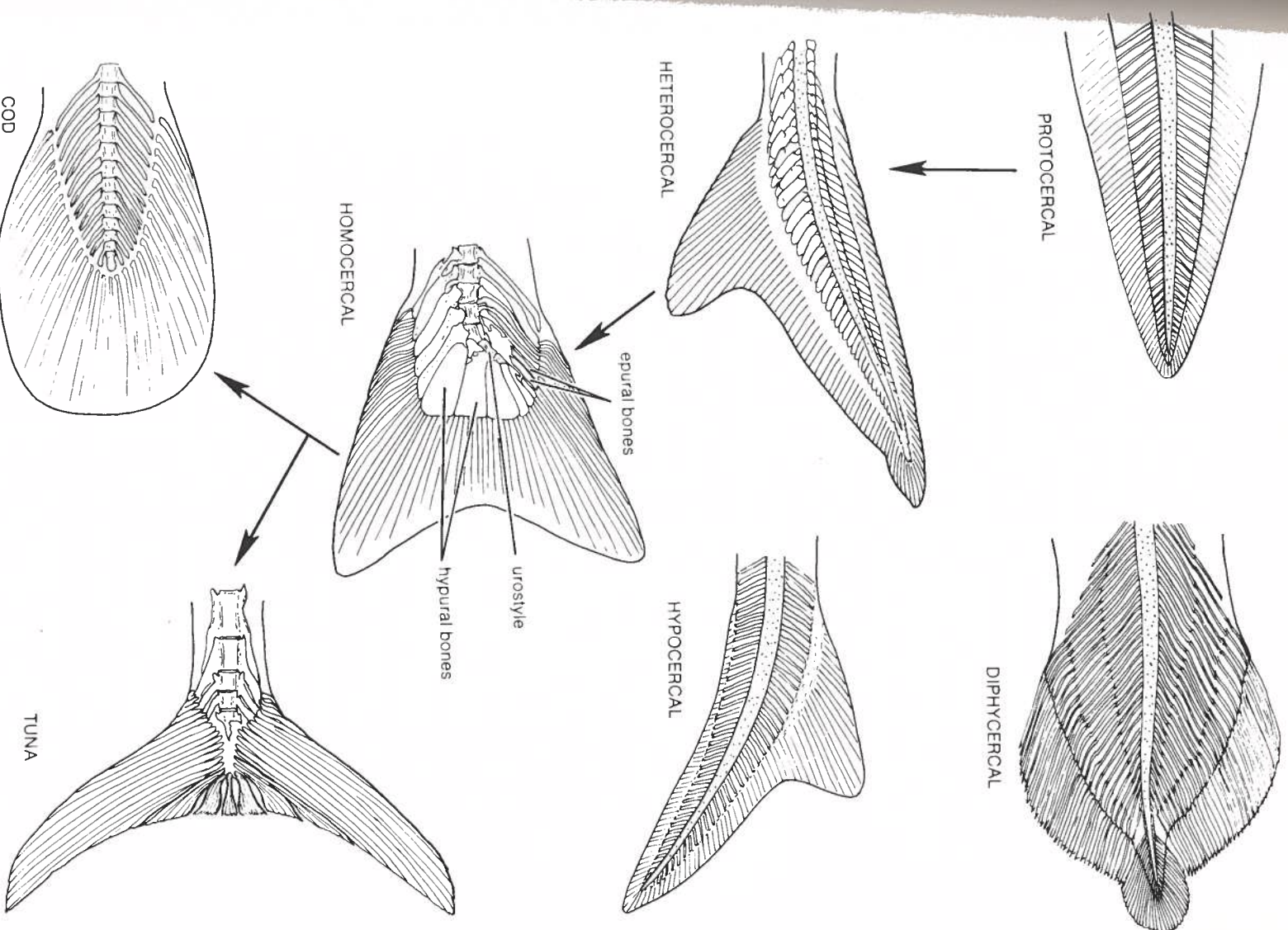


Fig. 6.14. Different kinds of tails found in various groups of fishes. Partly after Jollie 1962 (*Chordate morphology*. New York: Reinhold).

The transition from an aquatic to a terrestrial existence was accompanied by several modifications of the vertebral column and ribs. Whereas in fishes the major movements of the body were in a horizontal plane accompanying propulsive events, movements in terrestrial vertebrates in-

### 1. The Origins of Terrestrial Vertebrates

volve vertical as well as horizontal flexing. Further, the vertebral column becomes a weight-bearing members. As a consequence of these new functions, the notochord is replaced by the sequentially arranged centra as the major axial element, the intervertebral articulations are strengthened, and the ribs are greatly enlarged. The enlargement of the centra is accompanied by a steady decrease in the size and functional significance of the notochord. Zygapophyses, processes that join the neural arches of adjacent vertebrae, are enlarged, and the articulation is increased in extent and complexity. Not only do the zygapophyses increase the total strength of the articulated vertebral column, they enable the trunk to accommodate to the torsions accompanying quadrupedal locomotion. The ribs in the earliest terrestrial vertebrates were massive structures that supported the body during rest on land and prevented collapse of the abdomen while in the air. Probably the earliest terrestrial vertebrates dragged the abdomen and tail along the ground during their forays on land. Suspension of the trunk from the upright limbs and girdles was likely a rather late evolutionary development.

### 2. The Vertebral Columns of Early Amphibians

Almost from their first appearance the amphibians displayed a great diversity in the construction of the vertebral column. In terms of the general structural pattern, with centra, neural arches, ribs, and connections to the girdles, there was uniformity. The greatest diversity occurred in the structure of the centra and their relation to the other vertebral and rib elements. Amphibians are generally considered to have been derived from some group of rhipidistian fishes. Within known members of this latter group a moderate amount of vertebral centrum variation is seen. Usually there is a dominant element in each centrum, but this may be joined by a pair of moderate to small-sized elements that are now usually considered to represent the intercalary arches of archaic fishes. Thus the total centrum may have consisted of a rather large notochord with a single U- or O-shaped bony element surrounding it (fig. 6.15). In front of this element was a pair of intercalary bones having various structural features. In at least some rhipidistians (*Eusthenopteron*) this pair of bones was dorsal and bore traces of grooves that may represent the passage of the dorsal and ventral roots of the spinal nerves. These are considered by some authors to be homologues of the posterior pair of central elements in the early amphibians. Finally, some rhipidistians are known that have only a single central element and no accessory elements for each vertebra. Typically the neural arch is completely separated from the centrum in the fossil remains.

The earliest tetrapods (ichthyostegids) have vertebrae remarkably like those of some rhipidistians, including one dominant centrum element and a pair of accessory elements (fig. 6.15). These are often indicated as posterior centrum elements, but it is likely that they are homologues of the anterior accessory elements of rhipidistians. Many early labyrinthodonts have duplex centra, consisting of a U-shaped, dominant anterior bone and a pair of posterior, dorsally situated elements. The anterior bone is called the *intercentrum*, or the *hypocentrum*, and it usually forms the ventral support for the rib. The posterior pair of bones, the *pleurocentra*, and the neural arch, support the dorsal head of the

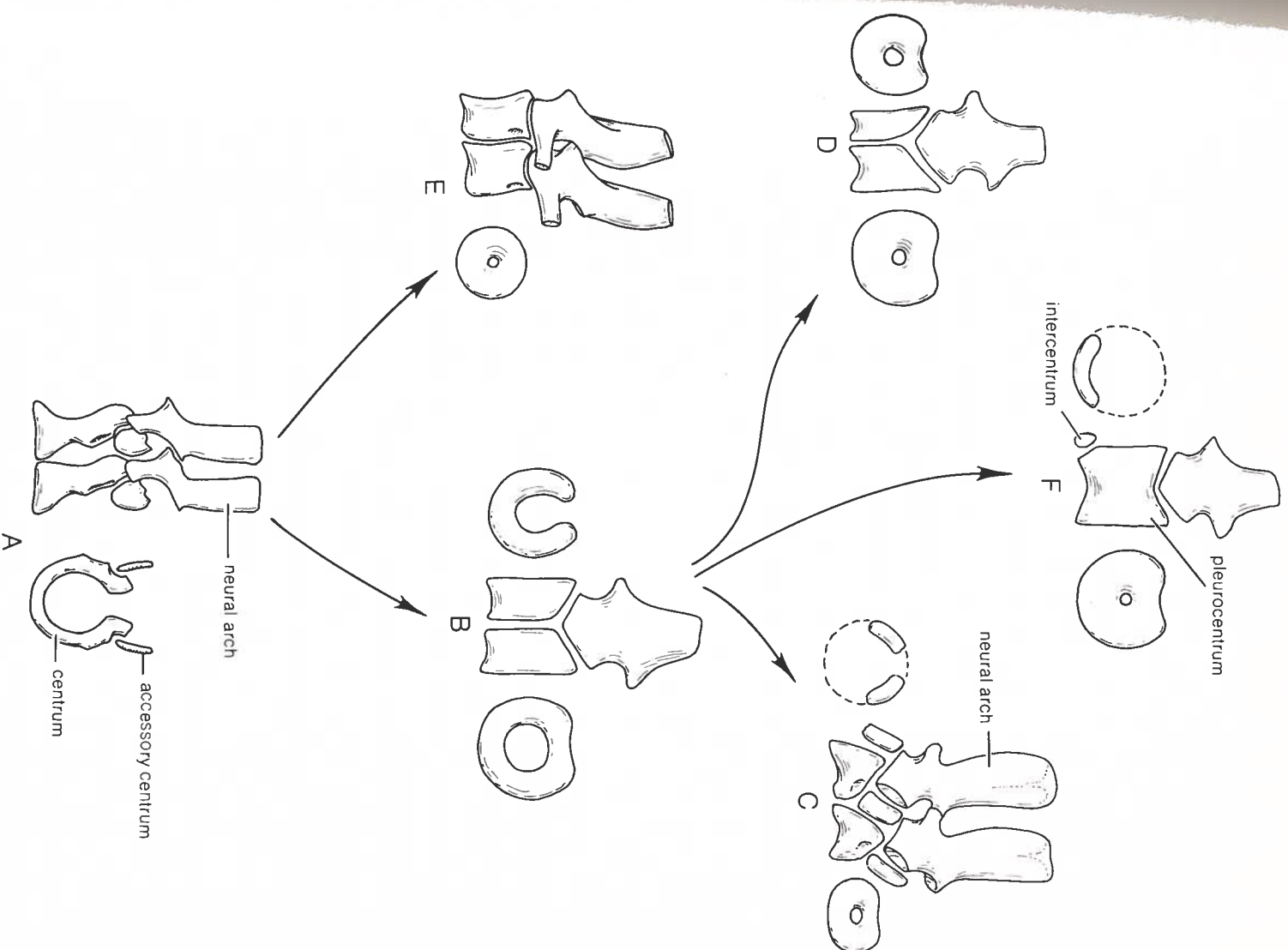


Fig. 6.15. Various tetrapod vertebrae. The vertebrae are shown in lateral view. Centra are also shown in cross section. *A*, a rhipidistian fish, *Eusthenopteron*. *B*, an early diplomerous amphibian. *C*, a rhaetomous amphibian. *D*, an embolomerous amphibian. *E*, a stereospondylous amphibian. *F*, an early reptile.

rib. The neural arch is a separate entity, more closely associated with the pleurocentrum than with the intercentrum.

For many years the classification of early amphibians has been based on the structure of the vertebral centra. The major types of vertebrae recognized are *rhacitomous*, in which a single U- or O-shaped intercentrum and a pair of usually smaller pleurocentra are present (fig. 6.15); *embolomeros*, in which a single U- or O-shaped intercentrum and a single U- or O-shaped pleurocentrum are present (fig. 6.15); *lepospondylous*, in which only a single centrum, not clearly homologous to either the inter- or pleurocentra is present (fig. 6.15); and *stereospondylous*, in which a single cylindrical intercentrum is present (fig. 6.15). The early amphibians with the most generalized structure (temnospondyls) have rhacitomous vertebrae, but in a few specialized groups (Dissorophoidea) the pleurocentra may be the dominant elements. Specialized late lineages of temnospondyls have stereospondylous vertebrae. In early members of the lineage of labyrinthodonts that gave rise to reptiles (anthracosaurs) the circular intercentra were the dominant elements, but in later members of the group the pleurocentra enlarge and fuse so that a duplex centrum is present with an adjacent intercentrum and pleurocentrum for each vertebra. In the ancestors of reptiles the intercentrum is reduced to a small ventral crescent, and the cylindrical pleurocentrum is the dominant element. Recent discoveries suggest that the pattern may not be as simple as presented here, but the major trends seem clear. Certain early amphibians were highly specialized upon their earliest appearance in the fossil record. These aistopods, neotridians, and some microsaurians have lepospondylous vertebrae similar in general to those of modern salamanders. The centra were thin, hollow cylinders with large anterior and posterior cone-like concavities. Presumably a notochord extended through the centra, and the concavities were filled by intervertebral cartilage that formed the articulations between adjacent centra. In some groups the neural arch was fused to the centrum, but in others (microsaurs) the two units were separate. In some microsaurians a small, crescent-shaped ventral element appears in an anterior position in the tail region, and it has been called an intercentrum. The presence of this element has led some workers to conclude that the dominant centrum in lepospondyls is a pleurocentrum. An extension of this logic has led to the identification of the single centrum of modern amphibians as a pleurocentrum. Supportive evidence is the similar development of the centrum in living amniotes, which clearly have a pleurocentrum based on paleontological grounds, and in the modern amphibians, whose ancestry is unknown. Not all workers accept this reasoning, arguing instead that the questions of ontogeny and phylogeny should be clearly separated until the ancestry of all living groups is clarified. According to this latter view, the centrum of the lepospondyls and modern amphibians, in its unitary state, is the homologue of the entire centrum unit, whether simple or compound, in the rhipidistians, the labyrinthodonts, and the amniotes.

### 3. Vertebral Column of Salamanders

Whole skeletons of salamanders, for example *Necturus*, *Cryptobranchius* or *Ambystoma*, are needed for this study. The vertebral column consists of five rather poorly differentiated regions. The *cervi-*

*cal* or *neck* region consists of a single vertebra, which lacks ribs and articulates with the skull by means of two large *coryles* (fig. 6.16). Note that a well-developed process, bearing articular facets, projects into the foramen magnum. This is the *tuberculum interglenoideum*, a feature unique to salamanders. The long *trunk* region consists of vertebrae that are generally similar in construction. All but the last usually bear ribs. From ten to more than sixty trunk vertebrae occur in different species. The *sacral* region consists of one vertebra, the *sacrum*, whose ribs, the *sacral ribs*, attach to and support the pelvic girdle. The *caudal* region is a transition from sacral to caudal vertebrae. From two to four vertebrae are present. They may bear ribs, but usually do not. The last caudal vertebra is recognized as the first vertebra to bear a well-developed hemal arch. This vertebra supports the posterior part of the cloaca and marks the end of the trunk. The *caudal* or *tail* region, composed of vertebrae lacking ribs and having hemal arches, contains from about twenty to more than one hundred vertebrae.

Study individual vertebrae. They are remarkably distinctive, with long, low neural arches fused to rather weak, amphicoelous centra. The tail vertebrae resemble those of fishes, having neural and hemal arches and a centrum that bears projecting lateral processes. On the trunk vertebrae the bicipital or two-headed ribs are attached to two lateral processes. The dorsal process, or *diapophysis*, arises near the midpoint of the neural arch and bears the dorsal rib head, or *tuberculum*. The ventral process, or *parapophysis*, arises from the dorsal part of the centrum, slightly anterior to the diapophysis, and supports the ventral rib head, or *capitulum*. The ribs appear to be the homologues of the dorsal ribs of fishes. In some species the rib heads are fused together. The tail can be autotomized in many salamander species, and some members of the family Plethodontidae have a marked basal tail constriction. There is no intravertebral autotomy septum and the break occurs between vertebrae.

The vertebrae are articulated to each other by *zygapophyses*, a pair of projections on the neural arch fitting over a similar pair on the anterior end of the succeeding vertebra. Thus each vertebra has a pair of *prezygapophyses* on its anterior end whose articulating surfaces face upward, and a pair of *postzygapophyses* on its posterior end whose articular surfaces face downward. An *intervertebral cartilage* forms the joint between adjacent centra. This spindle-shaped structure fits into the concavities in adjacent centra. Primitively a large notochord persists in salamanders, and it extends through the center of the centrum and the intervertebral cartilage. In more advanced species the notochord is reduced in size and importance, and the intervertebral cartilage is enlarged. This latter element consists primarily of hyaline cartilage and is firmly anchored into the anterior end of each vertebra. The joint is formed by a disk of fibrocartilage that arches anteriorly from the ends of the centra. Thus a kind of ball-and-socket joint is formed and the vertebrae are functionally *opisthocelous* (with a concavity anteriorly and a convexity posteriorly in the joint). In newts and some other salamanders the intervertebral cartilages may ossify to produce truly opisthocelous vertebrae.

#### 4. Vertebral Column of Frogs

Frogs have a single cervical vertebra that resembles that of salamanders in having two large articular facets and lacking ribs, but it also lacks the tuberculum interglenoideum. The trunk contains from four to eight (usually seven) vertebrae, succeeded by a single sacral vertebra. Behind the sacrum a long *urostyle*, derived from several fused postsacral vertebrae, completes the column; there is no tail (fig. 6.16). No hemal processes are present, and ribs are present in adults only in the most primitive frogs. Typically the vertebrae bear well developed *transverse processes*, and those of the sacrum, termed *scara diaphragyses*, have a variety of shapes. In some species they are rather simple cylindrical structures, while in others they may be extremely large and flattened, with great distal expansion. The sacral diapophyses support the enormously enlarged ilia of the pelvic girdle, which extend posteriorly. Much movement is possible at the sacroiliac joint, which appears to be in the middle of the back (fig. 6.16). Behind this point there is no flexibility and in front of it there is relatively little. What movement does occur is in the vertical plane.

The vertebral column in frogs is much compressed. The neural arches are low and short, with small zygapophyses. The centra have a variety of shapes, but generally they are larger and more solidified than in salamanders. The most primitive species have a persistent notochord and amphicoelous vertebrae, with the intervertebral cartilage forming the joint. A few species have opisthocelous vertebrae, but the vast majority are *procoelous*, with anterior convexity and posterior concavity (fig. 6.16). There may be variations in the form of the articulation, especially in the immediate presacral region. The centra may develop around the notochord, as in salamanders (*perichordal development*), or they may develop only from tissue that lies atop the notochord (*epichordal*), a unique pattern.

#### 5. Vertebral Column of Caecilians

Caecilians are limbless and very elongate, with virtually no tail. There is a single cervical vertebra with two large cotyles, which merge ventromedially to form an anterior process quite unlike that in salamanders. There are no cervical ribs. Following this are a series of from about 60 to 285 vertebrae. Most bear bicipital ribs, but these are absent in the cloacal region. There is no sacrum, and the cloacal vertebrae are irregularly shaped lumps of bone. In some features the vertebrae resemble those of salamanders, but they are highly distinctive, with stout centra and high neural arches. There are no hemal arches, save for some anomalous structures in the cloacal region. The pattern of the rib-bearers is especially distinctive. The diapophyses are borne on the anterior part of the neural arch, and the parapophyses are attached to the extreme anterior end of the centrum (fig. 6.16). The centra are amphicoelous, but the joint is formed from a ligament-like structure that joins adjacent vertebrae. This develops from an intervertebral cartilage that is very reduced in adults. The notochord is persistent but is replaced by a mineralized cartilage plug in the midpoint of each vertebra.

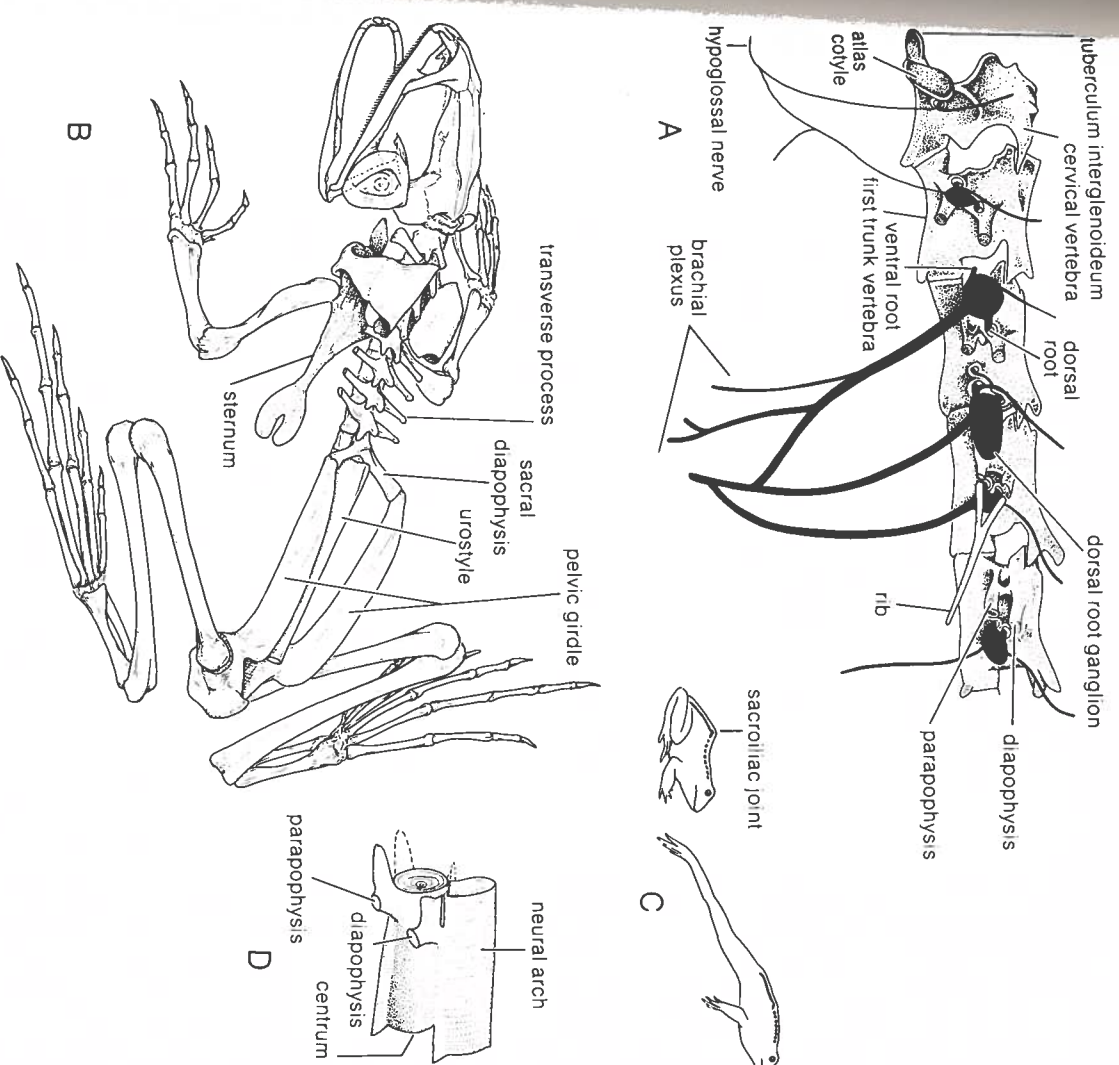


Fig. 6.16. Amphibian vertebral columns. *A*, the anterior part of a vertebral column in a plethodontid salamander, *Eurycea*, to show relation of spinal nerves to vertebrae, and vertebral joints (after Wake and Lawson 1973). *B*, the skeleton of a frog, *Rana*. *C*, a frog at rest (left) and jumping (right), to show great movement at the sacroiliac joint. *D*, a trunk vertebra of a caecilian.

#### 6. Development of the Vertebrae in Modern Amphibians

The three orders of living amphibians show few similarities in the mode of vertebral development. Caecilians have the most amniote-like development. Salamanders resemble caecilians in most aspects of development, but they have a very scanty sclerotome. Very little of the centrum is preformed in cartilage in the salamanders and caecilians. By contrast, frogs have much such preformation. The sclerotome is scanty in frogs, and the mode of vertebral development is unique.

## H. Vertebral Column of Reptiles and Amniotes in General

### 1. Primitive Reptilian and Amniote Vertebrae

The ancestry of reptiles is now reasonably well known, and the stages leading to the development of the typical amniote vertebrae can be documented. Amniotes evolved from a group of anthracosaur labyrinthodonts. This group had a vertebral column in which the pleurocentrum was the dominant centrum element and in which the intercentrum was being reduced in size with time. Thus the proximate amphibian ancestors of reptiles had vertebrae consisting of three distinct parts; the neural arch, a dominant pleurocentrum, and a rather small intercentrum. The pleurocentrum fused with the neural arch, and the intercentrum was reduced to a thin crescent of bone underlying the notochord at the anterior end of each vertebra by the time of the origin of reptiles. Thus the early reptiles, and living amniotes, have essentially monospondylous vertebrae, in which the dominant centrum element is the homologue of the pleurocentrum of ancient amphibians. The intercentrum is usually absent in living amniotes, but it may be present in the tail region, where it contributes to elements of the ventral arch termed *chevron bones*. These always lie at the anterior of the vertebra. Some primitive reptiles have persistent intercentra in the cervical region, but the elements are not typically present in amniotes. Some workers believe that the intervertebral cartilages or intervertebral disks incorporate part of the presumptive intercentrum.

### 2. Evolution of the Atlas and the Axis

The head and trunk of fishes move as a unit, and no specialized joint occurs between the two regions. One of the most striking evolutionary developments of land tetrapods is the craniovertebral joint. Its evolution is doubtless associated with land life, most obviously with sensory perception and feeding, but also with locomotion. Modern amphibians have a well-developed craniovertebral joint with a pair of specialized, convex, occipital condyles on the back of the skull articulating with a pair of enlarged articular facets on the first vertebra. The first vertebra of salamanders has a distinct anteriorly directed process, but the other amphibians lack such a structure. In the ancestors of reptiles the occipital condyle was a single median element, and it retains that morphology in modern reptiles. However, its articulations with the vertebral column are quite different than those of amphibians. The first two vertebrae (termed *atlas* and *axis*) of amniotes are usually modified for the support and movement of the skull (fig. 6.17). The atlas is a ring-shaped element that lacks a typical centrum. It bears one (reptiles and birds) or two (mammals) enlarged, concave articulating facets that receive the knob-like occipital condyle. The axis typically has an anteriorly projecting *odontoid process*, which extends into the base of the foramen magnum and acts as a pivot in the turning of the head. This process thus extends through the relatively short atlas. The most extreme development of this condition is in the mammals, and in many reptiles somewhat intermediate conditions are encountered. There is much controversy concerning exact homologies of the parts of the cervical vertebrae of amniotes. Evidence is good, however, that the definitive centrum of the atlas (the pleurocentrum) is fused to that of the axis to form the odontoid process. The exact composition of the ring-like part of the atlas that surrounds the odontoid is not clear, and it has been suggested that

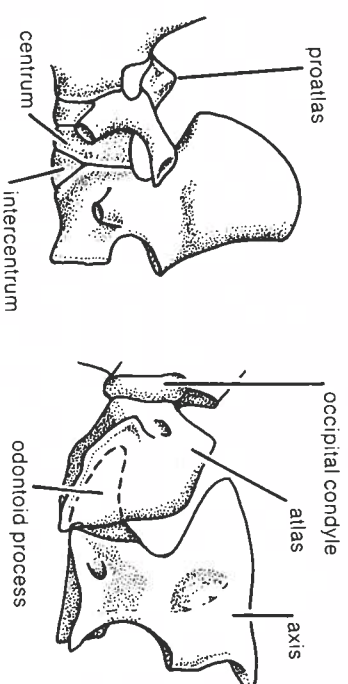


Fig. 6.17. The atlas-axis complex in amniotes (after Romer 1970 [*The Vertebrate Body*, Philadelphia: Saunders]). *A*, *Ophiacodon*, a primitive reptile. *B*, a generalized mammal. The broken line in *B* indicates the odontoid process of the axis, which is thought to be formed from the centrum and intercentrum of the more anterior vertebra of ancestral forms.

either the intercentrum, the ventral arch elements, or both contribute to its formation. Embryological evidence suggests that the odontoid process is an extension of the axis that includes not only the intercentrum of the axis but also the pleurocentrum of the atlas. In some reptiles an additional element, the *proatlas*, may be present between the atlas and the occipital arch. This was long thought to be the remnant of a "lost" vertebra, but it is now thought to be formed by tissue that might have formed the postzygapophyses of the occipital arch of ancestral forms.

### 3. The Tetrapod Rib

Land vertebrates have only a single pair of ribs for each vertebra, and these extend outward from the column, into the lateral trunk musculature, which is increasingly reduced in the higher vertebrates. These are now generally considered to be the equivalent of the dorsal ribs of fishes. Primarily ribs are borne on all vertebrae from the atlas well into the tail. Tetrapod ribs are typically two-headed (bicipital). Primarily the lower head, or *capitulum*, is the largest, and it articulates either directly or with a process (*parapophysis*) of the intercentrum. The upper head, the *tuberculum*, is weaker and articulates with a process (*diapophysis*) attached to the neural arch (fig. 6.18). Accordingly the lower head is ahead of the upper one. The prevailing theory considers the tuberculum and diapophysis to be derived from their more ventral, anterior counterparts. These structures are considered to have evolved in response to selective pressures associated with supportive requirements for terrestrial locomotion. As these organisms become more and more terrestrial, pressure points formed where the ribs were forced upward and toward the midline by the bulk of the abdominal mass. The rib-bearers presumably developed in response to such stimuli.

As the intercentrum was reduced in size, the articulation of the capitulum shifted anteriorly, so that it was supported by half-facets on two adjacent centra, or on the intervertebral disk. The typical situation in living tetrapods is the development of a parapophysis on the centrum, almost directly below the diapophysis, but there are many variations in the mode of rib articulation.

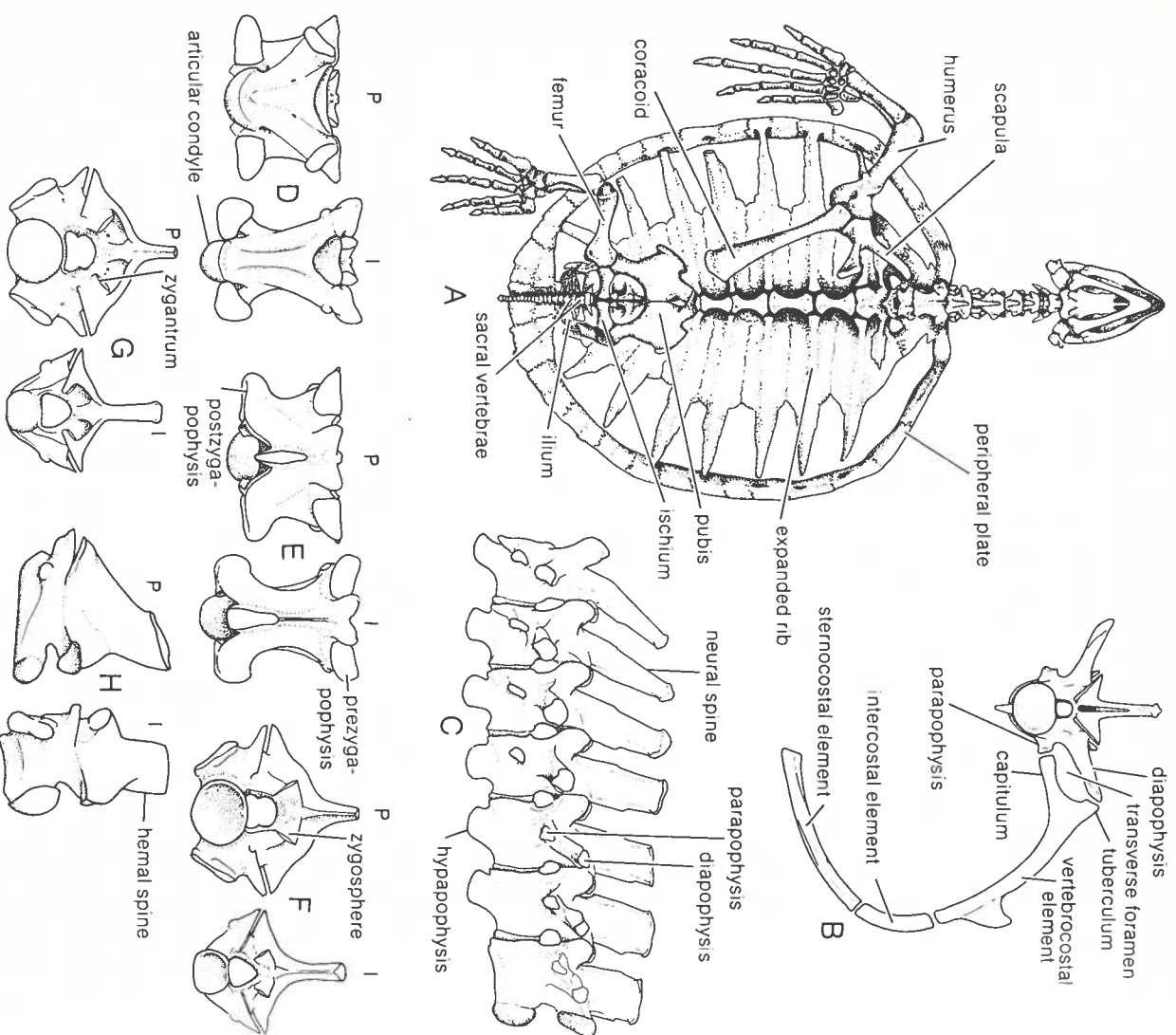


Fig. 6.18. Vertebrae of living reptiles. *A*, the skeleton of a sea turtle, viewed ventrally (after Bellairs 1969 [*The life of reptiles*: London: Weidenfeld and Nicolson]). *B*, the vertebral column of an alligator, in cross section (after Hoffstetter and Gasc 1969). *C*, portions of the neck and trunk of a crocodile, in lateral view (after Hoffstetter and Gasc 1969). *D*, ventral, *E*, dorsal, *F*, anterior, *G*, posterior, and *H*, lateral, views of trunk vertebrae of a snake (*Python*, *P*) and a lizard (*Iguana*, *I*) (after Hoffstetter and Gasc 1969).

The early tetrapods had movable ribs along most of the vertebral column, but the more posterior of these fused to their bearers to form pleurapophyses. This pattern has continued into the modern tetrapods, which rarely have postsacral ribs. Usually ribs are small and short in the flexible neck region. Those of the thorax play an important respiratory role in many amniotes, and they are usually imbedded in the body wall musculature. There they curve around to the ventral surface, and articulate with the sternum. They become divided into two or three sections for greater flexibility, usually an upper bony vertebral section and a lower cartilaginous sternal or costal section. Ribs of the lumbar region are incorporated into laterally extending pleurapophyses or, if articulated, greatly reduced in size. The sacral ribs, one or more pairs, attach the pelvic girdle to the vertebral column and are usually short, stout, and nearly immovable.

In modern reptiles two-headed ribs are present only in the crocodylians. The ribs of snakes are very important in locomotion, and they function in conjunction with the elaborately differentiated trunk musculature and enlarged ventral scales. These ribs are long and curved over most of the presacral region. In turtles only ten pairs of ribs are present, and usually the middle eight are distally expanded to contribute importantly to the carapace. The ribs extend from the vertebral column laterally to the dermal skeleton of the shell, forming a flying buttress that strengthens the carapace.

#### 4. Abdominal Ribs

Ventral or abdominal ribs, also called *gastralia*, are imbedded in the ventral wall of the trunk in many fossil and recent amphibians and reptiles. These are often dermal elements that are usually V-shaped, with the apex directed anteriorly. Homologies are not clear, and there have been suggestions that distinction should be made between those that have a typical dermal bone ossification pattern and those that preform in cartilage and even remain so in the adult. These latter elements probably gave rise to the sternum.

#### 5. Development of Amniote Vertebrae

Embryos of amniotes are richly supplied with sclerotome, and this purely embryonic tissue plays a dominant role in the formation of the vertebra. The sclerotome is organized in distinct repeating units, corresponding exactly with the myotomal segmentation. These masses of cells should be viewed as dynamic entities, not as blocks of inert material. They fill a large part of the area between the myotomes and the notochord and nerve cord and are separated from each other by areas of markedly lowered cell density rather than by discrete boundaries. The limits of the cell masses are marked by the intersegmental blood vessels, and these may serve as convenient landmarks for study of later stages. An extension of the myocoel—the sclerocoel—has been described in some amniotes, but recent studies have questioned its reality. It is said to lie approximately in the center of each sclerotomal mass, separating the relatively cell-poor cranial half from the cell-rich caudal half.

The first stage in development of the adult vertebra involves a movement of mesenchymal cells around the notochord. These cells multiply

to produce condensations near the middle of each segment. The areas between condensations gradually fill with cells and a more or less continuous perichordal tube results that surrounds nearly the full length of the notochord.

After the production of the perichordal tube, a period of rapid differentiation ensues. The areas of condensation in the tube, known as the perichordal rings, are destined to become the intercentrum, or the intervertebral cartilage. The cells that span the old intersegmental fissure will give rise to the adult centrum, the homologue of the pleurocentrum of early tetrapods. Rudiments of the neural arch now appear immediately above the centrum. At first these are represented by basal condensations, but growth is rapid and the condensations prolong around the nerve cord. This tissue typically lies in front of the intersegmental blood vessels and is derived mainly if not exclusively from cells of the caudal sclerotome half. A condensation of cells forms dorsolaterally between adjacent neural arches and unites them. It is in this mass of cells that the zygapophyses form.

Nearly all of the vertebra of amniotes is preformed in cartilage, which is very important as a growth tissue in the rapidly changing element. Differentiation of the intercentra and intervertebral disks proceeds, and the centrum is fully distinguished from them. The centrum chondrifies separately from the neural arch, and a neurocentral suture of rather undifferentiated tissue persists for a long while. The neural arch becomes complete over the nerve cord, and the zygapophyses appear.

Growth of the centrum is much more rapid than growth of the intercentrum and intervertebral cartilage. Incorporation of intervertebral cartilages into the intercentrum is typical of most amniotes. The definitive intervertebral joint forms in the remnant of the intervertebral tissue near the center of each segment.

Ossification of the vertebra is basically a matter of endochondral osteogenesis, but some tissue immediately in front of and behind the cartilaginous core of the neural arch (neural pedicle) ossifies directly. Typically the adult vertebrae are heavily ossified structures containing little cartilage. As in many amphibians, the notochord may persist in some small lizards, and it may contain plugs of cartilage at the midvertebral level. In addition, in *Sphenodon* and in some lizards the intervertebral cartilage remains in a cartilaginous state. When the cartilage does not mineralize, the vertebrae are said to be amphicoelous, even though the presence of the cartilage makes most vertebrae functionally procoelous. Most reptiles are procoelous, though there are many modifications. Birds and mammals have special patterns of intervertebral articulation.

## 6. Vertebral Column of Crocodilians

Regional differentiation is rather well marked in crocodilians. There are nine cervical vertebrae, distinguished by ribs that fail to reach the sternum. The first two cervical vertebrae, the atlas and the axis, consist of separate components. The atlas is a ring composed of four bones, the paired neural arches and dorsal (proatlas) and ventral (intercentrum) connecting pieces. The proatlas is probably the remnant of an ancient zygapophysal joint between the occipital and atlantal arches. The in-

tercentrum bears a pair of long movable ribs with single heads. Although the centrum of the atlas is apparently absent, embryological evidence indicates that it has fused with that of the axis, forming the odontoid process. The craniovertebral joint is formed by the unpaired occipital condyle and the hollowed parts of the intercentrum and neural pedicels of the atlas. The axis has no free intercentrum. Strong neural arches and elongated neural spines characterize the axis and succeeding cervical vertebrae, and the ribs are rather short and double-headed. From the short ribs of the axis to the long ones of the last cervical vertebra, rib length steadily increases. Distinctive, short midventral projections (*tyrappophyses*) are present on the centrum of the cervical and anterior trunk vertebrae (fig. 6.18C). Ligaments extending between these suspend the neck and are important in support of the massive head.

The next fifteen vertebrae form a distinct functional unit, the trunk. The first eight or nine of these bear trisegmented ribs that reach the ventral surface of the body and form the thoracic basket. Ribs of the first two arise from bearers that are well separated, as on the cervicals, and connect directly with the sternal plate. The bearers and rib heads enclose a large opening, the *transverse foramen* (fig. 6.18B). The successive openings form the *vertebrarterial canal*, in which blood vessels to the head are situated. Ribs of the next three vertebrae consist of one or two segments only. The trunk vertebrae that bear ribs are often called thoracic vertebrae, and the last three or four, which have long transverse processes but no free ribs, are termed lumbar vertebrae.

Crocodilians have two sacral vertebrae, each of which bears stout ribs that articulate with the ilia. The first postsacral vertebra differs from all other vertebrae in having a biconvex (most are procoelous) centrum. It also lacks a hemal arch and is thus a transitional or caudosacral vertebra. The first eighteen caudal vertebrae have intercentral hemal arches, formed by the chevron bones, and transverse processes. The last few caudal vertebrae are strongly compressed and lack transverse processes. The shape of the caudal vertebrae reflects the use of the tail in locomotion, which is accomplished by strong lateral movements. Differences in the orientation of the zygapophyses can also be noted, and those of the trunk tend to restrict movement and increase rigidity, while those of the tail favor lateral bending.

## 7. Vertebral Column of Turtles

All turtles have thirteen presacral vertebrae. The cervical vertebrae, always eight in number, are movable and usually have only vestigial ribs or no ribs at all. Most turtles that fold their necks in a vertical plane (Cryptodira) have a very generalized atlas-axis complex. The atlas typically consists of three separate parts, the intercentrum, the centrum, and the neural arch. In the side-necked turtles (Pleurodira), which fold their necks in a horizontal plane, and in some others, the separate elements tend to fuse, and a distinctive, large atlas may result. The cervical vertebrae behind the axis are very flexibly articulated, with well-developed ball-and-socket joints that are differently organized in different families. These differences reflect differences in the mode of neck movement. The trunk, or dorsal, vertebrae are intimately associated with the carapace, each corresponding to a medial dermal shield (fig. 6.18A).



Neural arches tend to be displaced forward to an intercentral position, to agree in conformation with the original segmentation pattern. Ribs of the middle eight trunk vertebrae join the carapace in all but one family (*Dermochelyidae*). The ribs are usually intercentral in position. They expand and fuse to the inner surface of the costal plates of the carapace. Ordinarily there are no special articulations between the trunk vertebrae. The nineteenth and twentieth vertebrae are the sacrals in most turtles, but the region is not well defined in pleurodirres. The sacral ribs, and in some groups the last one or two ribs of the trunk vertebrae, meet the ilia. The tail vertebrae articulate freely and are usually procoelous. They are small and few in number. A few anterior vertebrae in the tail may bear ribs. In some species the neural arch is separated from the centrum by a narrow cartilage band. Small hemal arches and in some instances chevron bones are present.

### 9. The Vertebral Column of *Sphenodon*

This genus has the most primitive reptilian vertebral column among living forms. The notochord is persistent and the vertebrae are amphicoelus. A small intercentrum is present in all but the cervical vertebrae. There are eight cervical, seventeen trunk, two sacral, and twenty-nine to thirty-six caudal vertebrae. The elements of the atlas remain separate, and there is a small proatlas. The centrum of the atlas is fused with that of the axis, which in turn fuses or articulates with intercentra of the first three vertebrae. The last five cervical vertebrae bear ribs of increasing length. The trunk vertebrae bear well-developed ribs that are modified so as to be not quite two-headed. The first three trunk ribs reach the sternum, and some of the more posterior ribs attach to the gastralia by connective tissue. Ribs of the last three trunk vertebrae are short. The result of this pattern is the formation of a thoracic cage anteriorly and a slight tendency toward a waist posteriorly. The sacral vertebrae have strong ribs. Anterior caudal vertebrae are well developed but bear no ribs. The first three postsacral vertebrae are transitional in morphology and have normal intercentra. In more posterior vertebrae the intercentra are modified to form chevron bones, which are part of the hemal arch.

The tail can be autotomized. This is accomplished by a break in specialized tail vertebrae. The region of the break corresponds to the embryonic borders of the sclerotomes. The border region remains unossified, forming a relatively weak transverse autotomic septum. This first appears on the eighth caudal vertebra.

### 10. The Vertebral Column of Lizards

Lizards are a diverse group with great variation in the numbers of vertebrae. There is a general structural similarity, however, and lizard vertebrae are rather distinct from those of other reptilian groups. Many geckos have amphicoelous centra, but the great majority of lizards are procoelous. Intercentra are typically present only in the cervical region. The number of presacral vertebrae seems to be about twenty-four in most lizards, but dwarf chameleons have as few as sixteen, and some limbless lizards may have as many as 116. Many lizards have eight cervical vertebrae, the last five of which bear increasingly elongate ribs. The first trunk vertebra is the one whose ribs contact the sternum. The atlas is a ring formed of the neural arch articulated to a hypapophysis

(ventral process of a centrum) or to an intercentrum. The axis includes the centra of both the atlas and axis. Typically intercentra are present in the cervical region but not in the trunk region. Two intercentra may be fused to the axis, or they may be free. Ribs of about the first five trunk vertebrae are joined to the sternum or xiphisternum. Most trunk vertebrae bear a pair of single-headed ribs, but a few immediately in front of the sacrum may lack them. Some families of lizards have secondary articulation surfaces on the dorsal part of the neural arch, between the zygapophyses. These are termed *zygosphenes* (on anterior end of vertebra) and *zygantra* (facets on the posterior end of the vertebra, which receive the zygosphenes) (fig. 6.18). There are two sacral vertebrae, usually fused. The enlarged sacral transverse processes articulate directly with the ilia. They incorporate embryonic rib rudiments. Usually one to four *pygal* or caudosacral vertebrae lie between the sacral and caudal regions. The first caudal vertebra bears a hemal arch in the form of a chevron bone, which incorporates the intercentrum. There are no free postsacral ribs. Most lizard families have autotomic septa in several to many caudal vertebrae and are capable of tail autotomy. The break occurs midvertebrally as in *Sphenodon*, but the details differ in a taxonomically significant way from family to family (fig. 6.19).

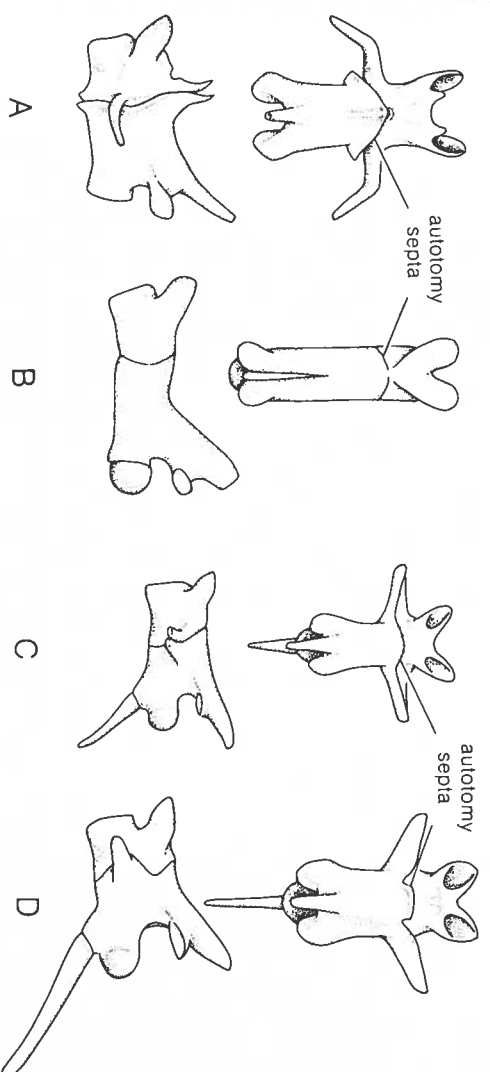


Fig. 6.19. Caudal vertebrae of lizards, to show autotomy septa. Dorsal (top) and lateral (bottom) views (after Hoffstetter and Gasc 1969 and Etheridge 1967). *A*, a gecko; *B*, an iguaniid; *C*, a scincid lizard, *Scincus*; *D*, a scincid lizard, *Lygosoma*.

### 11. The Vertebral Column of Snakes

The vertebral column of snakes is rather similar in structure to that of *Sphenodon* and lizards, but in its lack of precise regional differentiation and its complex articulations it reflects its role as the major locomotor organ. Musculature of the snake body is extraordinarily complex, with precisely organized tendinous attachments to the vertebrae that vary greatly from one taxonomic group to the next. It is the combination of multiple joints (many vertebrae and long, double-headed ribs) and complex musculature that enables snakes to move in such varied and

intricate ways. The atlas-axis complex is much like that of lizards. Other cervical vertebrae cannot be distinguished from trunk vertebrae. From 160 to more than 400 vertebrae are present, and the great majority are preclacal. The individual vertebrae typically are stout and well developed (fig. 6.18). The centrum ranges from very short to very long, relative to lizards. Centra are strongly procoelous, with stout, protrusive posterior condyles. Zygosphenes and zygantra are well developed. Frequently, well-developed hypapophyses are present on the ventral surface of the centrum. Ribs are typically long, robust, and well ossified. There is no sternum, and all ribs have free ends, with rather stumpy tips. Ribs in the cloacal region are forked. There are no postcloacal ribs. Hemapophyses appear in the cloacal region and are distinctive in that they are separated distally. Thus the hernal arches are incomplete. Only a very few species are capable of tail autotomy, and they have autotomic septa, similar to those in lizards, in a few caudal vertebrae.

Compare these features among reptilian skeletons available for study.

### I. Vertebral Column of Birds

Birds display great similarity in the structure of their vertebral columns, which are highly specialized as a result of adaptations for flight. Reduction of vertebral flexibility, except in the neck, is a striking feature of the bird vertebral column. This reduces intervertebral movement during the flight, hence reducing frictional loss of energy. The most striking feature is the fusion of numerous vertebrae with the pelvic girdle to form a weight-bearing synsacrum in the posterior part of the body. The column is rather short, with a total of nearly forty to more than sixty vertebrae (fig. 6.20). No free intercentra occur in adults, but embryonic rudiments contribute to the atlas, axis, and pygostyle. The atlas is very similar to that of mammals but seems to have been independently derived. It is a ring-shaped element that lacks a centrum. Embryological evidence indicates that the centrum of the atlas fuses with that of the axis to form the odontoid process. The atlas and the axis articulate with the unpaired occipital condyle. In hornbills the atlas and axis are fused, but this is an exceptional situation. The cervical vertebrae are those anterior members of the column that lack ribs, or whose ribs do not articulate with the sternum. The number is variable (from eleven to twenty-five, but usually thirteen to sixteen). Generally the longer-necked birds have high numbers of cervical vertebrae. The thoracic vertebrae bear ribs that reach the sacrum, and they usually number four to five (from three to ten). Varying degrees of fusion of the thoracic vertebrae occur, and frequently the middle three form a single unit. In some species one or two cervical vertebrae may be fused to this mass. The synsacral mass incorporates a number of vertebrae (ten to twenty-two), and several subregions, based on vertebral components, can be recognized. The thoracic synsacrum fuses to the ilia by means of dorsal and ventral rib-bearers, and the first of the series usually bears a small rib. Elements of the lumbar synsacrum are fused to the ilia by the ventral rib-bearers only, the dorsal bearers having been lost. The primary synsacrum is composed of from zero to three vertebrae that are fused to the ilia by dorsal and larger ventral rib-bearers. The ventral bearer incorporates a

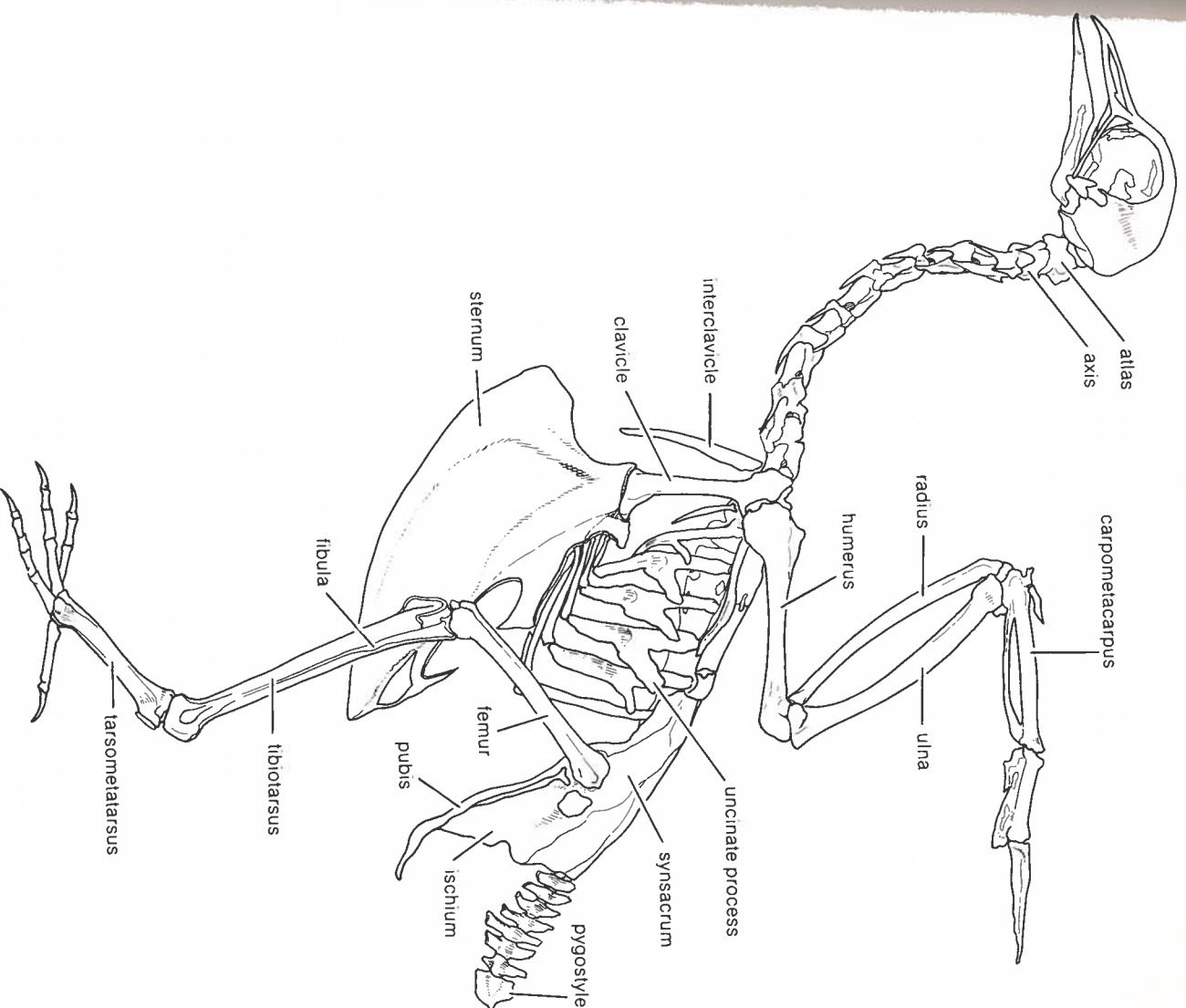


Fig. 6.20. Skeleton of a pigeon. After Petingill 1956 (*Ornithology*. Minneapolis: Burgess).

sacral rib. The caudal synsacrum includes two to ten vertebrae, united to the ilia by often rather stout transverse processes. The caudal vertebrae usually number six (three to twelve) that are free, and from four to seven additional vertebrae that are fused to form the pygostyle. The pygostyle serves as the base of attachment of the long tail feathers, or retrices, that are of great locomotory and behavioral importance in birds. In ancient

birds (*Archaeopteryx*) a long tail, composed of regular caudal vertebrae, was present, but in modern birds this is reduced to a small, but very important, stump. Hemal arches are absent on all caudal vertebrae.

Although most of the bird vertebral column is characterized by rigidity, that portion of it that is vertical, the neck, has great flexibility. Most birds can turn their heads nearly 180° in either direction. This flexibility results from the saddle-shaped, or heterocoelous, centrum ends (fig. 6.4), which should be examined on isolated neck vertebrae. These articulations are unique among vertebrates in the extent of movement permitted.

The ribs of birds are divisible into the usual vertebral and sternal sections. The vertebral portions bear posteriorly directed uncinate processes that are a characteristic avian feature. These processes form bridges between adjacent ribs and strengthen the rib cage.

## J. Vertebral Column of Mammals

### 1. The Cervical Vertebrae

The vertebral column of mammals is differentiated into five regions, and the typical vertebrae of each region are sufficiently distinct to be readily identifiable when isolated. The following description applies primarily to articulated skeletons and isolated vertebrae of cats and rabbits.

Typically mammals have seven cervical vertebrae, the first two of which are differentiated to form the atlas and axis. Sloths have six to nine and sirenians have six cervicals, but even such long-necked forms as giraffes retain the generalized number of seven. In aquatic mammals with short necks, such as whales and dolphins, the vertebral centra are very short and often more or less fused. Fusions also occur in armadillos and in such ricochetal rodents as kangaroo rats and jerboas (fig. 6.21). Some believe that fusions in these rapidly moving rodents reduce head-bobbing during locomotion. The atlas is a ring-shaped bone with wide, wing-like lateral projections. These projections represent ribs, and they are perforated by the vertebralarterial canal. In monotremes the sutures between the cervical ribs and the processes of the centrum are evident in young animals, and this is also true of some young dogs. Typically, however, the sutures disappear. The low, flat neural arch of the atlas is perforated for the passage of the first spinal nerve, a situation also encountered in lower vertebrates. The anterior surface of the atlas has a pair of large, curved concavities that articulate with the paired occipital condyles of the skull. As in reptiles, the atlas consists mainly of the bases of the neural arch, but the median ventral region is produced by the intercentrum rudiment. A separate intercentrum occurs in the atlas of some marsupials, but in most it is replaced by a ligament.

The axis has a large and elongated neural arch with a forward-projecting neural spine. Zygapophyses first appear on its posterior border. The odontoid process extends from the anterior end of the centrum of the axis into the ring of the atlas and is important in rotation of the head on the neck. The odontoid develops from the centrum of the atlas embryologically, as in reptiles. The axis and succeeding cervical vertebrae have transverse processes that are formed in part of ribs fused to their rudimentary bearers. All but the last are pierced by the

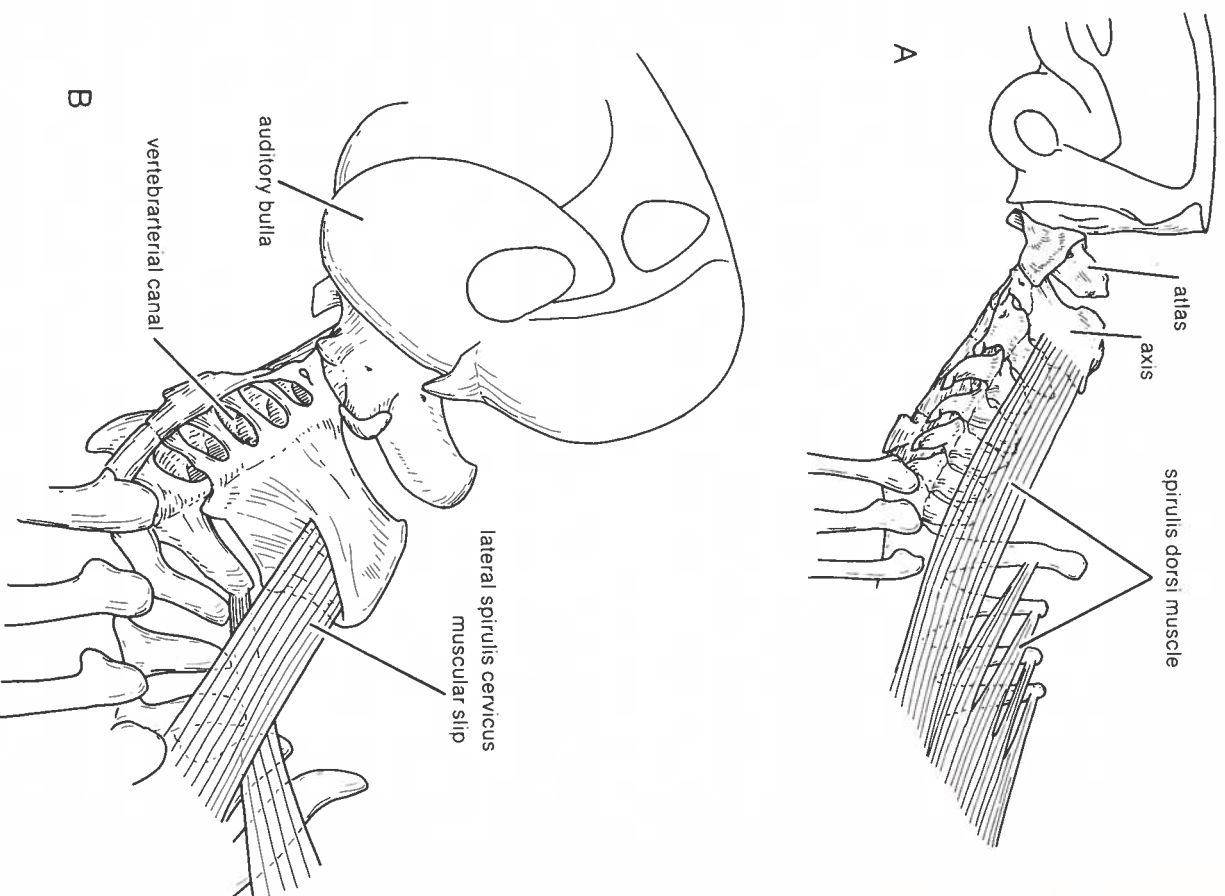


Fig. 6.21. Neck region of mammals (after Hatt 1932 [Bull. Am. Mus. Nat. Hist. 63:599-738]). *A*, *Rattus*, to show the general mammalian condition. *B*, *Jaculus*, a Jerboa, to show the fused sacral vertebrae found in some ricochetal rodents.

vertebrarterial canal, a feature that distinguishes cervical from thoracic vertebrae.

The remaining cervical vertebrae are similar in general form, with well-developed neural arches and spines, pre- and postzygapophyses and transverse processes. The prezygapophyses are distinguished from the postzygapophyses by dorsal, as opposed to ventral, orientation of the articular surfaces.

## 2. The Thoracic Vertebrae

These rib-bearing vertebrae are recognized by the presence of costal facets for rib articulation. Cats have thirteen, and rabbits usually twelve, thoracic vertebrae; the number varies from group to group. The commonest numbers are twelve to fifteen (twelve in man). Cetaceans have the fewest (nine) and sloths the most (up to twenty-five). Often the anterior thoracic vertebrae have very tall neural spines that are directed caudad, short centra, small pre- and postzygapophyses, and short, stout transverse processes. The ribs articulate with the transverse processes, or diapophyses, by their upper heads. The lower heads of the ribs articulate between the centra, where the intracentra of ancestral forms occurred, but partial facets for articulation are found on the anterior end of the centra and the epiphyses. The epiphyses of two articulating vertebrae, plus the *meniscus*, or articular pad, between them, seem to be homologues of the intervertebral disk of lower vertebrates, and possibly also of the intercentra.

The last thoracic vertebrae differ somewhat from the others in having reduced neural spines and transverse processes, more prominent zygapophyses, a single rib facet, and an extra process from the pre-zygapophysis, termed the *metapophysis* or *mammillary process*.

## 3. The Ribs

The ribs of mammals typically consist of a bony vertebral rib and a cartilaginous sternal rib or costal cartilage. The tuberculum diminishes in size posteriorly, and the last ribs (three in the cat) have only capitular heads. The narrowest part of the rib between the two heads is termed the *neck*; the remainder of the rib, the *shaft*; and the point of greatest curvature of the shaft, the *angle*. Ribs that have an independent attachment to the sternum are *true ribs*; those that join the preceding ribs or are unattached ventrally are called *false ribs*; the unattached false ribs are known as *floating ribs*. Cats have nine true and four false ribs, of which the last is floating; man and rabbits have seven true and five false ribs, three floating in rabbits and two in man. In sirenians and whalebone whales all but the first one to three ribs are floating. Only monotremes and some sloths have three-sectioned ribs, and it is not clear that these correspond to the divisions of reptilian ribs. Uncinate processes are lacking in mammals but are present in many of their therapsid ancestors. The ribs of anteaters, some armadillos and a few slow-moving arboreal primates (lorisids) have expanded, overlapping ribs. These increase the stability of the thorax, and hence of the vertebral column. This is important in trunk stabilization during underground activity, or in methodical arboreal locomotion. Some arboreal anteaters anchor themselves with their hind limbs and tail and extend

the trunk to reach an adjacent branch with outstretched forelimbs; this requires much trunk stability.

## 4. The Lumbar Vertebrae

From four to seven (the latter typical of cats and rabbits) lumbar vertebrae are usually present in mammals, but monotremes and some edentates have from two to four, and as many as twenty-one occur in cetaceans. The lumbar vertebrae are large and stout, with prominent neural spines and long, anteriorly directed transverse processes. These processes typically include rib rudiments and are hence called *pleurapophyses*. A prominent metapophysis projects above the prezygapophyses, and a spine-like *anapophysis* (*accessory process*) is seen below the postzygapophyses.

## 5. The Sacrum

The sacrum is composed of a variable number (three in cats, usually four in rabbits, five in man) of fused vertebrae that articulate with the ilia. From six to eight sacral vertebrae occur in some perissodactyls, and up to thirteen are found among edentates. Typically the first assumes the greatest part of pelvic girdle support, and it has large lateral expansions. These incorporate the sacral ribs, which are indistinguishably fused to the vertebra.

## 6. The Caudal Vertebrae

A highly variable number of caudal vertebrae occur in mammals, usually corresponding with tail length (up to fifty in long-tailed forms, but usually only three to five, fused to form the coccyx, in man). Neural arches, transverse processes, and zygapophyses diminish caudally, and the last vertebrae consist only of centra. Chevron bones are commonly present, and very small ones, often lost, in skeletal preparation, occur in cats. Some mammals are capable of tail autotomy to a slight degree, but regeneration is limited to completion of the broken vertebra and wound healing, in contrast to the situation in reptiles and amphibians.

## 7. Functional Consideration

The work of Slijper has provided new perspectives for studies of the functional morphology of the vertebral column in mammals, and the two paragraphs that follow, quoted from his work, admirably summarize his outlook (see fig. 6.22).

"The body-axis (vertebral column and spinal musculature) of mammals may neither be compared to an arched roof, nor to a bridge. In the first place it forms part of the construction of the whole trunk-skeleton. This construction may be considered as an elastic bow (pelvis and body-axis of the trunk) bent in the dorsal direction (ventral concave) by a string (sternum, abdominal muscles, linea alba, extrinsic muscles of the legs). The head and neck may be compared to a loaded beam supported at one end only. On the other hand, the whole body-axis may be compared to such a beam if the animal stands or sits on its hind quarters only, a posture that is attained by every mammal now and then. Thus the principal static function of the body-axis is to resist bending in the dorsal direction. The elastic resistance is caused by the strength of the intervertebral discs and ligaments, but chiefly by the tonus of the epaxial musculature.

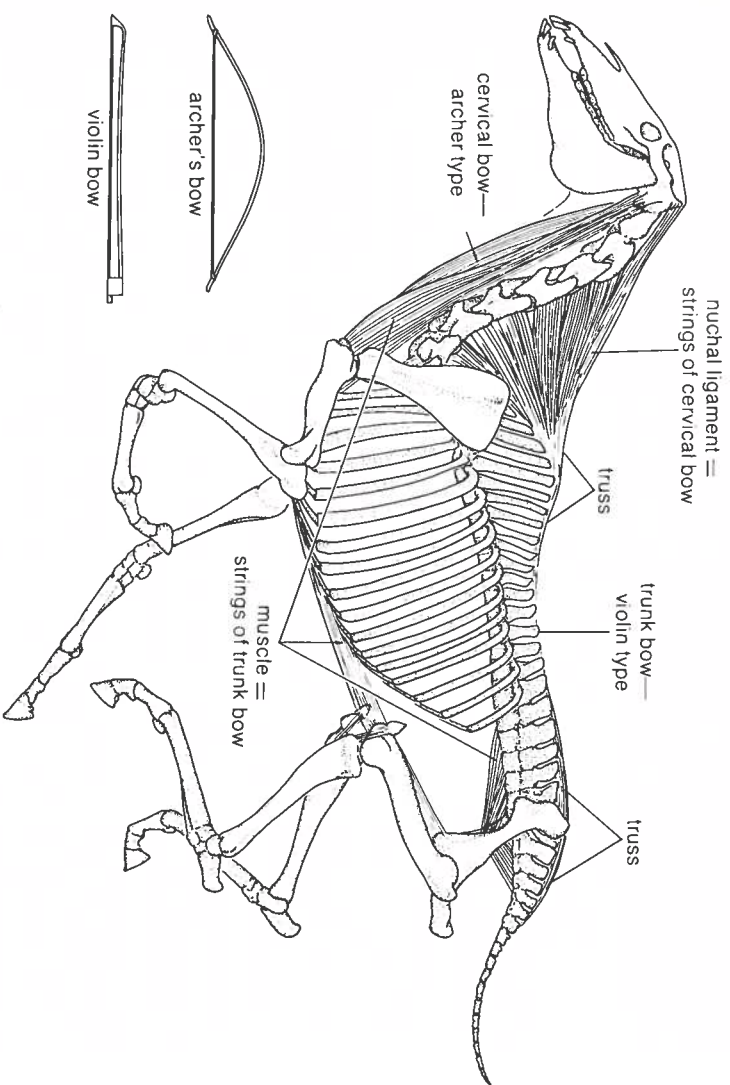


Fig. 6.22. A running horse, to show features of the functional dynamics of the spine in relation to the head and limbs.

"In the second place the body-axis is an organ of locomotion. It has to transmit the locomotive power from the hind quarters to the forehead (this means chiefly to resist bending in the dorsal direction) and it has to bend and extend the back in the sagittal plane, especially when the animal moves in a leaping-gallop."

Mammals differ from fishes, amphibians and reptiles in the reduction of lateral flexion as an important component of the locomotory pattern. The vertebral column of a generalized mammal, such as the cat, is far more flexible in the sagittal plane than in the frontal plane. Further, secondarily aquatic mammals, unlike secondarily aquatic reptiles, never use side-to-side swimming motions of the body. Rather, they engage in a dorsoventral movement of the body axis.

Among cursorial terrestrial mammals two extremes of adaptation in the vertebral column are observed. Compare with the adaptations mentioned in chapter 7. These correspond to the two extremes of running patterns. The highly flexible body axis of such forms as the cheetah is characteristic of sprinters. The lumbar region is long and the neural spines of more anterior vertebrae are relatively short. Much dorsoventral movement is possible. In contrast, the vertebral column of cursorial ungulates, which have considerable staying power while running, has a relatively short lumbar region, tall anterior neural spines, and almost no flexibility.

There are functional reasons for these differences. A sprinting mammal expends much energy to attain high speed quickly. The flexible back

of the cheetah is in effect an extra set of muscles and an extra joint segment to the hind legs, which in the cheetah are the primary propellers. By flexing and extending its trunk in addition to accelerating its legs, the cheetah moves most of its mass through a great distance with each stride. It pays a high price in terms of energy expenditure.

In contrast, running ungulates require endurance and have evolved adaptations that permit high speed with relatively low energy expenditure. The rigidity of the back precludes moving the body mass great distances in the sagittal plane, and this saves energy. The forelimbs are principally involved in steering, but propulsive power, though generated mainly by the hind limbs, comes from them as well.

Richochetal (leaping) mammals have vertebral columns similar to those of sprinters, in part because the main propulsive force is from the hindquarters. However, the anterior parts of the vertebral column tend to be much reduced and the cervical vertebrae may fuse, in contrast to the situation seen in such sprinters as cats.

Burrowing mammals tend to have highly flexible vertebral columns, for they must be able to turn around in their burrows. Arboreal mammals that are very active (monkeys) have a flexible column, but those that are slow and deliberate (sloths, lorises) have very rigid backs.

#### K. Summary

1. The vertebral column develops around the notochord, a stiffened rod that extends from the region of the braincase to near the end of the tail. The complex notochordal sheath includes several layers of fibers surrounding the vacuolated notochordal cells. The notochord has enough resilience to serve as the main axial support and locomotor organ in *Branchiostoma*, in some primitive fishes, and in the early larval stages of modern amphibians. In most vertebrates the notochord is either replaced by or incorporated into the developing vertebrae.
2. Vertebrae form at the intersections of myotomes, and they have a pattern of repetition that is about one-half cycle out of phase from the segmentation of the body. This pattern is imposed by the functional necessity to bend the body axis, thus creating waves for locomotion. It is not necessary to postulate any highly mechanistic explanation for the formation of vertebrae in particular positions. The neural arch develops somewhat independently from the centrum, especially in lower vertebrates. In fishes the centrum forms from a series of centers, some originally serving as bases for the neural arch, others forming from notochordal materials, and others forming from mesenchyme in the area. These centers are interrelated in different ways in different vertebrates, with some having all centers and others only one. Most higher vertebrates show only so-called auto centers, which form in mesenchyme surrounding the notochord.
3. Ribs are formed along the margins of most vertebrae in fishes and along the trunk vertebrae of tetrapods. Both intermuscular ribs, which lie at the intersection of each myoseptum with the horizontal skeletalgenous septum, and subperitoneal ribs, which lie against the coelomic lining, are present in many fishes. In other fishes and in tetrapods, only the first group is present.

4. The vertebral columns of cyclostomes and some archaic fishes are very poorly developed. In some instances it is evident that the skeleton is less well developed than in ancestral forms, and there seems to be a trend in the direction of skeletal reduction. Such is the case in lungfishes and *Latimeria*, for example.
5. Cartilaginous fishes have well-developed vertebral columns, composed of complexes of skeletal plates that form a continuous skeletal tube.
6. Modern bony fishes have vertebrae that differ strikingly from those of archaic and cartilaginous fishes. The vertebrae are typically very well ossified and have a variety of specialized processes. Each group has vertebrae that have evolved specialized structure in relation to mechanical demands resulting from locomotor adaptations.
7. Related to the vertebral column are the endoskeletal fin supports of the median and tail fins in fishes. These form two extremes of structure, rigid spines and flexible rays. The rays of the tail fin are arranged in a variety of patterns, reflecting phylogenetic history and function.
8. Early amphibians initially had vertebrae not much different from those of lobe-finned fishes, but as terrestrial adaptation proceeded the vertebral centra diversified greatly. Zygapophyses evolved between the neural arches, and a variety of articulations between adjacent centra appeared. The centra consisted of two major parts, often called intercentrum and pleurocentrum, in different proportions among different groups. In some groups, notably the lepospondyls, there is only a single element in the centrum.
9. The modern amphibians are similar in vertebral structure in that a single unitary vertebra forms, with no separation of the neural arch and the single centrum. There are many differences among the three major groups. Salamanders have the most generalized vertebrae, with a distinct tail and paired ribs along the trunk vertebrae. Caecilians have only a vestigial tail and the ribs have a curious anterior placement on each of the very numerous trunk vertebrae. Frogs have extremely shortened vertebral columns, with rudimentary ribs present in only a few primitive species; a specialized urostyle forms during development from vertebral rudiments. The development of the vertebrae is distinctive for each of the three groups.
10. Amniotes all share a similar pattern of vertebral development, but it is a matter of controversy whether a distinct resegmentation occurs. Rudiments of a second centrum are found in the chevron bones of the tails of some living reptiles, but the main centrum is thought to be homologous with the pleurocentrum of ancient amphibians and reptiles.
11. A distinct neck region is present in all amniotes, and a specialization of the first two vertebrae to form the atlas and axis has occurred independently in several different lines. The odontoid process of the atlas forms in a very different manner than does the similarly shaped tuberculum interglenoideum of modern amphibians.

12. Tetrapod ribs are thought to be the equivalent of the intermuscular or dorsal ribs of fishes. Characteristically each rib is two-headed. Some modern and many fossil reptiles and amphibians also have abdominal ribs, termed gastralia. These are dermal elements embedded in the ventral body wall that develop independently of the vertebral column.
13. Each of the living reptilian groups has distinctive vertebral columns. This is especially true of the turtles, in which the trunk vertebrae are incorporated into the carapace of the shell. In many lizards and in snakes there are accessory articulations between the adjacent vertebrae associated with specialized locomotory modes. Specialized autotomy planes are present within the tail vertebrae of many different lizards and amphisbaenians, and some snakes.
14. Birds' vertebral columns feature variable numbers of neck vertebrae and fusions of other vertebrae into complexes of bone associated with attachments of enlarged muscles related to locomotion.
15. The mammalian vertebral column is well differentiated into five regions, and vertebrae from each are easily identified by their shapes as to position and function. Mammals with specialized modes of locomotion may show modifications of parts of the vertebral column. For example, the cervical vertebrae of different jumping rodents are fused. Ribs of some climbing, slow-moving species overlap, thus providing stability for the thoracic region. Ribs are borne on thoracic vertebrae, and these are followed by a series of ribless lumbar vertebrae. Different numbers of vertebrae are incorporated into the relatively complex sacral region, and tails vary greatly in length.
16. Vertebral columns play important functional roles in static support as well as dynamic support during movement. In many groups the vertebral column is the organ of locomotion. Thus in lower vertebrates waves are propagated at the anterior end of the vertebral column and these travel down the body axis, applying force to the medium or substrate and propelling the animal forward. Usually this wave is generated simply by differential contraction of the segmental musculature. However, in lizards and especially in snakes there are many additional, highly specialized muscles that are involved in bending the vertebral column and transmitting force to the external scalation. In addition to traveling waves, terrestrial vertebrates are capable of propagating waves that "stand" in one position on the column, causing one part of the body to oscillate. These waves are found at the junctures of the pectoral and pelvic girdles to the vertebral column where they cause the girdles, and their associated limb elements, to move in anterior-posterior planes. In this manner waves propagated along the vertebral column contribute directly to increased stride length. In many groups of vertebrates (birds, frogs, many mammals) wave propagation is insignificant or does not occur. However, movements in other planes may be significant. Dorsal-ventral movements of the column contribute to the jumping mechanisms of frogs and to the increased stride length associated with relatively great speed of such mammals as the cheetah. Finally, there are groups in which the vertebral column becomes a rigid supporting member during

locomotion in a way that suggests that the rigidity itself is an adaptation. This seems to be the case with large mammals, where lateral shifts of the massive bodies would require great energy expenditures.

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HYMAN ERRATA

Chapter 6

- p. 192 line 11 anterior should be posterior
- p. 193 line 4 notochordal
- p. 194 line 8 myotomes<sub>1</sub>
- p. 195 para. 2 line 5 enclosing ; Fig. 6.3 D tuberculum and capitulum lines should go to rib heads, not the dia- and parapophyses of the vertebrae
- p. 198 line 4 enclosed
- p. 207 para. 1 line 5 encloses ; para. 2 line 2 vertebrae are...
- p. 208 para. 2 line 2 delete (p. 00); last line amphicoelous
- p. 209 para. 2 line 3 enclose
- p. 210 para 4 line 2 coelacanth
- p. 212 line 2 ...member~~s~~.
- p. 214 para. 2 lines 3 and 11 rhachitomous
- p. 215 para. 3 line 4 prezygapophyses ; line 17 ...convexity anteriorly and concavity posteriorly... para. 2 line 2 amphicoelous
- p. 216 para. 1 indent first line; para. 1 line 9 sacral diapophyses  
para. 2 lines 7-8 ..anterior concavity and posterior convexity...
- p. 217 para. 1 line 6 much of such
- p. 219 para. 2 line 14 requirement
- p. 220 Fig. 6. 18 F. zygosphene H. neural, not hemal spine
- p. 223 para. 4 line 1 have eighteen...
- p. 224 line 3 ...middle ten trunk vertebrae... para. 2 line 3 ...coelous  
para. 2 line 1 8. not 9.; para. 3 line 1 9., not 10 etc.
- p. 226 para. 2 line 5 ...~~the~~ flight... line 21 sternum, not sacrum
- p. 227 Fig. 6.20 interclavicle should be clavicle; clavicle should be coracoid
- p. 229 Fig. 6.21 line 3 of legend sacral should be cervical; spirulis cervici
- p. 230 para. 4 line 16 Delete "The ribs of..."; capitalize Anteaters
- p. 235 para. 2 line 7 amphisbaenians
- p. 236 Baur reference ...Neugliederung...



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