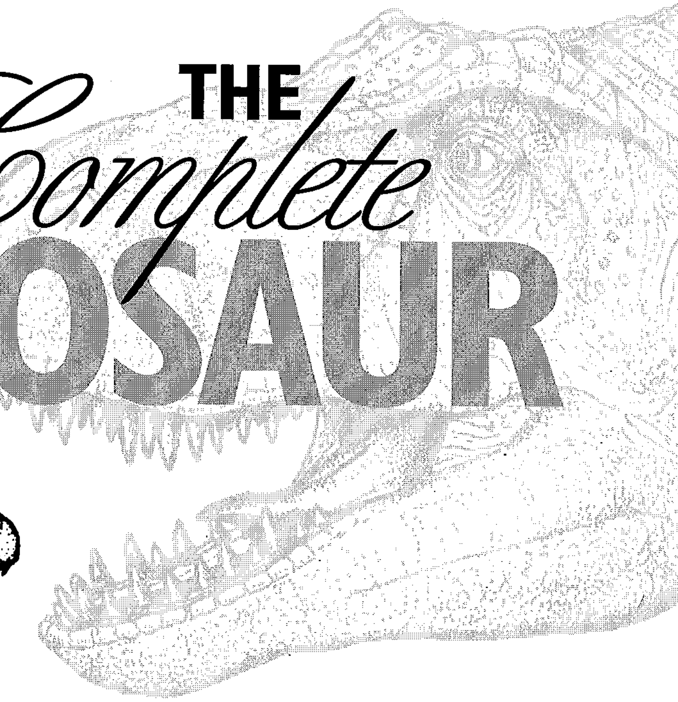
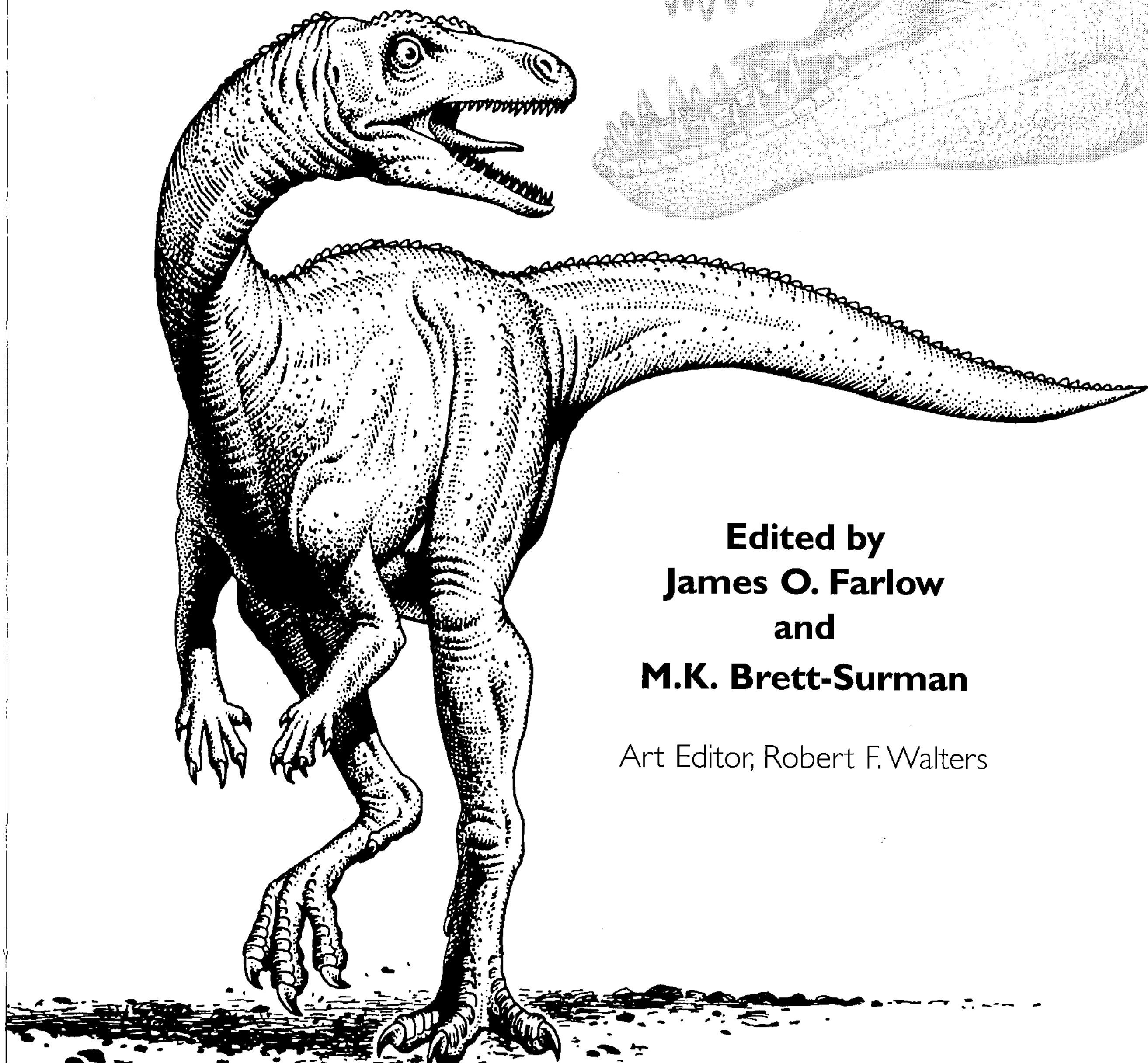
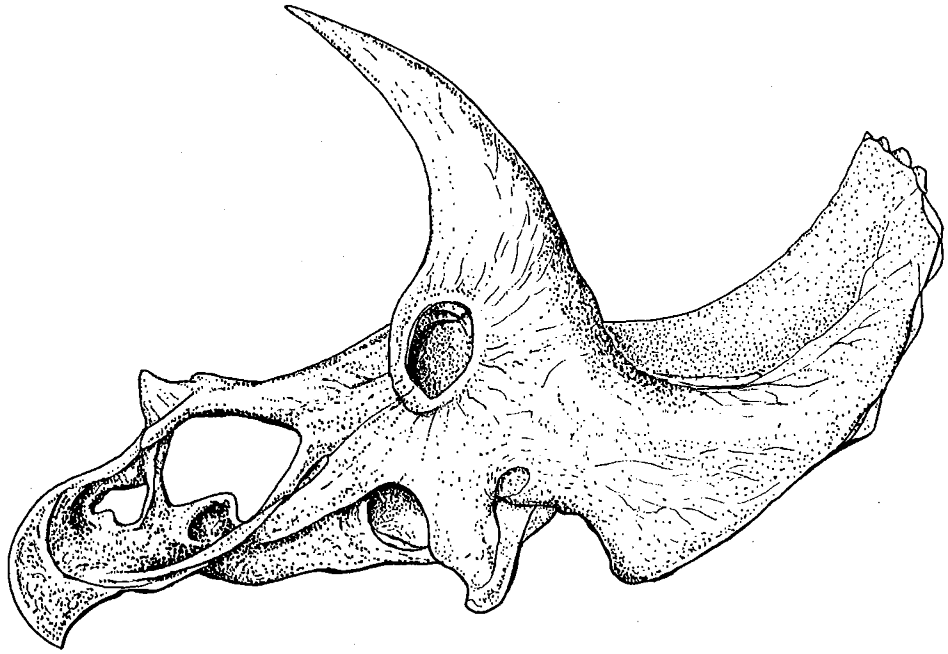
THE *Complete* DINOSAUR





Edited by
James O. Farlow
and
M.K. Brett-Surman

Art Editor, Robert F. Walters



The Osteology of the Dinosaurs

Thomas R. Holtz, Jr., and
M. K. Brett-Surman

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Dinosaurs are known only by their bones and teeth in most cases. The soft parts of the body, the skin, muscles, and other organs, were destroyed by decay processes fairly quickly after death. Only bones and teeth, the hard mineralized parts of a dinosaur, are durable enough to be preserved over tens of millions of years. Except for footprints, and much rarer traces such as eggs and skin impressions, fossilized skeletal material represents the only physical remains of the ancient dinosaurs. Thus the osteology (the study of bones) of dinosaurs is our main source of knowledge about these extinct animals.

Dinosaurs are tetrapod vertebrates—in other words, animals with bony skeletons and four limbs. All tetrapods, including amphibians, mammals, turtles, lizards, and birds, are built along the same general body plan. For example, the forelimb, or arm, of all tetrapods has one upper arm bone closest to the body, two bones below the elbow, several small bones in the wrists, and then a series of longer finger bones. (In some animals, such as snakes, the forelimbs have disappeared, but the ancestors of these animals had arms of the basic structure.) The reason all these animals share this common body plan is that all are descended from the same ancestral stock with that plan: the differences between the particular shapes of the bones arise from the same body plan having been modified, or adapted, to different uses (for example, the wings in birds or bats, the digging claws of moles, the grasping hand of a *Velociraptor,* or the pillar-like forefoot of a *Brachiosaurus*). Because of this common descent, we can recognize bones that are homologous; that is, they represent bones descended from the same original structure. Thus the upper arm bone of any tetrapod is homologous to the upper arm bone of any other tetrapod.

For an example of homology, compare the right hand of a human and the right "forepaw" of the plant-eating dinosaur *Iguanodon* (Fig. 7.1). These hands are oriented in the same direction, with the back of the hand facing us and the palm facing away. In the dinosaur, the homologue to the thumb has been fused into a large pike. The last digit, homologous to the "pinky" of a human, has evolved into an opposable finger. Opposability (the ability to place the digit on the palm) is characteristic of the thumbs of humans. Two different anatomical features in two different animals which have the same function but which are evolved from different parts of the body are called analogous. Thus the opposable digit of the *Iguanodon* is analogous to the human thumb, but homologous to the human pinky.

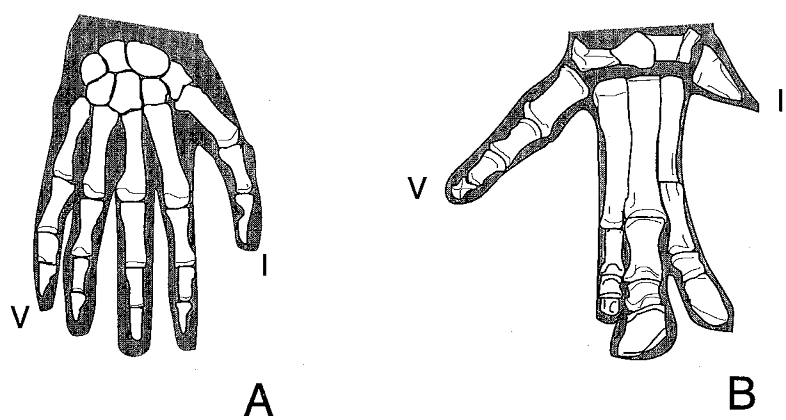


Figure 7.1. The right hands (manus) of (A) a human (*Homo sapiens*) and (B) the herbivorous dinosaur *Iguanodon mantelli* in anterior view. The spike in the hand of *Iguanodon* is homologous to (occupies the same anatomical position as) the human thumb. The opposable digit in the hand of *Iguanodon* is homologous to the human "pinky" but is analogous to (has the same function as) the human thumb.

It must be noted that in comparative anatomy the term *homologous* was not originally used in an evolutionary context. Sir Richard Owen, who coined the term *Dinosauria* in 1842 (see Torrens, chap. 14 of this volume), is also responsible for the use of homology in an anatomical context. Owen (1846, 1849) believed that for each major group of organisms there was a single basic body plan or "blueprint," of which all species in that group are variations. This body plan, the archetype, was not considered to have ever existed in the physical universe, but was a mental construct representing the simplified anatomical organization of each major group of organisms, such as vertebrates, mollusks, or insects. In this context the pectoral fin of a trout, the wings of birds, the forelimbs of horses, and the arms of humans were considered homologous since each was a variation of the same structure in the vertebrate archetype.

Sir Charles Darwin and his primary advocate, Thomas Henry Huxley, co-opted the concept of homology into the new theory of evolution by means of natural selection. In their view, where all animals of the same body plan have a common origin, a homologous structure in two or more organisms represents variations of the same structure that was present in a real common ancestor. (See Desmond 1982 for a detailed discussion of the social and political as well as the scientific conflict between Owen and Huxley over the concepts of "archetypes" and "ancestors.")

Anatomical Names, Directions, and Views

Because the basic bony anatomy, or skeleton, of all tetrapods is based on an ancestral body plan, all homologous bones can be given the same name. Since the anatomists who coined the various names used the classical languages Latin and Greek for scientific discourse, as did naturalists, astronomers, and other early scientists, most of these bones are named in Latin. Similarly, other structures in the skeleton (such as the socket for the eye or for the nostril) are also given Latin names.

In the past, many bones were given up to three sets of names. The bones of the body were first formally named in the human skeleton. Another, more general, set of names was applied to the mammals because they were historically the next group to be scientifically studied. Finally the "lower" vertebrates, such as lizards, crocodiles, birds, and amphibians, were given another, often simpler, set of names. For example, the main portion of the human cheekbone is a single unit called the os zygoma (*os* is Latin for "bone"; *zygoma* is Greek for "cheek"). In mammals, this bone is also called the os zygoma, more commonly just the zygoma. In all other vertebrates it is known as the os jugale (or more commonly just the jugal). However, with some rare exceptions (such as the zygoma/jugal), modern anatomists now use the same names for the homologous structures in all vertebrate species. For some details on the anatomical names in various tetrapod groups, see the *Nomina Anatomica* (1983) for human anatomy, the *Nomina Anatomica Veterinaria* (1983) for general mammalian skeletons, and Baumel and Witmer 1993 for bird osteology.

Before some of the important bones and other structures in the skeleton of dinosaurs are described, the principle of anatomical direction should be discussed. In order to describe the positional relationships of bones to one another in the skeleton of an animal, a series of pairs of directions has been invented. Like "north" and "south," or "up" and "down," these directions always have an opposite, pointing the other way. Unlike "north" and "south" and "up" and "down," however, these directions are not based on the external environment. Instead, they are internal to each organism, regardless of how it may move about in the outside world. The names are based on the standard posture of most tetrapods (that is, all forelimbs on the ground, head pointing forward, belly toward the floor and back toward the ceiling), so that the homologous directions in a human being (with only our feet on the floor, our face pointing the same direction as our belly, our belly pointed forward, and our backs pointed behind us) are oriented in somewhat different external directions. However, a crawling baby is oriented in essentially the same position as most other tetrapods.

The first pair of these are anterior (sometimes called cranial) and posterior (sometimes called caudal). *Anterior* means "toward the tip of the snout," and *posterior* means "toward the tip of the tail." For example, the shoulders are anterior to the hips, the skull is anterior to the neck, and the nostrils are anterior to the eye sockets. Conversely, the hips are posterior to the shoulders, the neck posterior to the skull, and the eye sockets posterior to the nostrils. Because these terms are independent of the external environment, they remain the same regardless of the position an animal is in (i.e., if a cat curls up, its tail is still posterior to the skull).

A second pair of anatomical directions is dorsal and ventral. *Dorsal* means "toward, and beyond, the spine" (or more simply "up"), while *ventral* means "toward, and beyond, the belly" (or, generally, "down"). In the skull, the teeth are ventral to the eyes, and the upper jaw is dorsal to the lower jaw.

The next pair of directions, medial and lateral, refer to directions relative to an imaginary plane through the center of the body, which runs from the tip of the snout through the tip of the tail, bisecting the body into a right and a left half. These two directions refer to the relative positions of bones to each other and to this imaginary midline. *Medial* refers to bones or structures which are closer to the midline (i.e., closer to the center), and *lateral* means farther away from the midline (i.e., farther out, or more right or more left). The shoulder blades are lateral to the ribs, and the spine is medial to the ribs.

A last pair is used primarily for directions within the limbs (the arms and legs) and is sometimes applied to the tail. *Proximal* means "closer to the trunk," while *distal* means "farther out from the trunk." For example, the hip is proximal to the knee, and the wrist is distal to the elbow.

Although these four pairs, anterior/posterior, dorsal/ventral, medial/lateral, and proximal/distal, are generally used to describe the relationships of bones to one another, they can also be used adverbially to describe how an anatomical structure is constructed. For example, the teeth of the upper jaw point ventrally, the snout of most animals projects anteriorly from the eyes, and the ischium (a bone of the hip) points posteroventrally (back and down) in all dinosaurs.

The names of the anatomical directions can be used to describe the particular surface of the bone illustrated in a photograph or drawing. To see the dorsal anatomical view of the skull, for example, means to see the top surface. The ventral view would be a picture of the bottom of a bone or skeleton, the anterior view the front, the posterior view the back. There is both a right lateral and a left lateral view of the skeleton, depending on whether you are viewing the right or left, respectively, of the animal. A medial view would show the surface of a bone which normally faces the midline.

In the following section, we will examine the major bones in the skeletons of dinosaurs. Drawings of various dinosaurs are used to illustrate the position and general shape of these bones. However, the Dinosauria were a very diverse group of animals, so there is considerable variation in the details of their skeletons. Elsewhere in this book you will find drawings of the osteology of the different dinosaur groups.

Sections of the Skeleton

The Skull

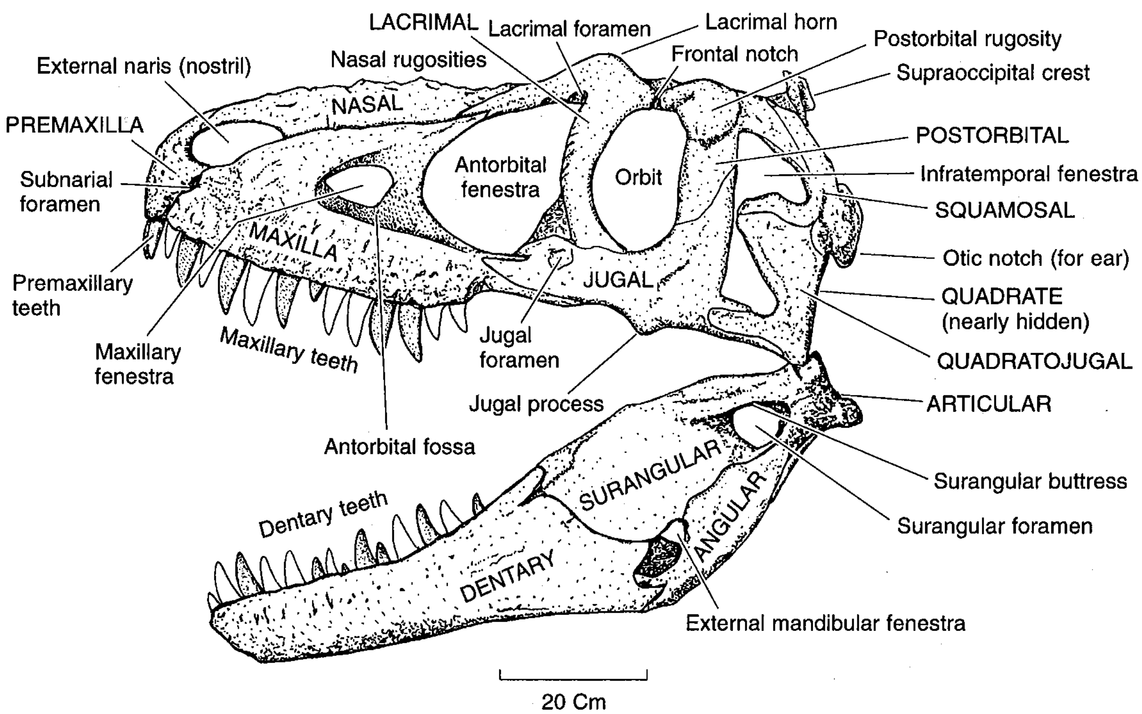
The skeleton of a dinosaur, or other tetrapod, can be divided into two main divisions: the skull, which refers to all the bones and teeth of the head, and everything else. The skull is mostly composed of many different bones which, like most of the bones of the body, are paired (i.e., there is one of those bones on the left side of the skull and one on the right side of the skull). There are also bones, though, which are single, and these usually lie on the midline. For example, the supraoccipital bone is right above the hole where the spinal cord enters the skull, and it is not paired. The outlines of the individual bones of the skull are recognized as sutures, where the different bones meet.

The skull itself is divided into two major sections. The upper part of the skull, including the eyes, nostrils, upper jaw, and braincase, is called the cranium (plural *crania*). The lower jaw is composed of the left and right mandibles.

It is sometimes easiest to recognize the different individual bones of the skull by starting out with non-bony landmarks. Landmarks are particular homologous features which are recognizable from animal to animal. Two of the best landmarks are the eye sockets and the nostril openings. The technical term for the eye socket is the orbit, while each individual nostril is called a naris (plural *nares*).

Among the other landmarks of the skull are the teeth. Made of materials (dentine and enamel) even tougher and more durable than true bone, teeth occur only on particular bones of the skull. In the dinosaurian upper jaw are two tooth-bearing bones. The most anterior is the premaxilla, and the posterior one (which is almost always much larger) is the maxilla. The premaxilla is ventral to the naris, and the maxilla is ventral to another opening. This opening is called the antorbital fenestra (plural *fenestrae*), literally "the window anterior to the orbit." This opening is found in many dinosaurs and their closest relatives. In the beaked, ornithischian ("bird-hipped") dinosaurs, the antorbital fenestrae are very reduced or entirely closed over, while in the saurischian ("lizard-hipped") dinosaurs these fenestrae are often very large. The antorbital fenestra sits in a depression, the antorbital fossa (plural *fossae*). In some advanced meat-eating dinosaurs, there are additional openings anterior to the antorbital fenestra. These are called the maxillary fenestra (or sometimes the accessory antorbital fenestra) and the promaxillary fenestra (which is more anterior on the inside of the antorbital fenestra and cannot be seen in this figure). Figure 7.2 illustrates most of these landmarks on the skull of the tyrant dinosaur *Daspletosaurus*.

Figure 7.2. The skull of the tyrant dinosaur (tyrannosaurid) *Daspletosaurus torosus* in left lateral view, illustrating the important bones (in CAPITALS) and landmarks of the skull. The subnarial foramen is a character found only in the Saurischia, and the maxillary fenestra and jugal foramen are unique to certain members of the Theropoda. The nasal rugosities, frontal notch, jugal process, and surangular buttress are specializations of tyrant dinosaurs, and are not found in most dinosaurs. Illustration by Tracy Ford.



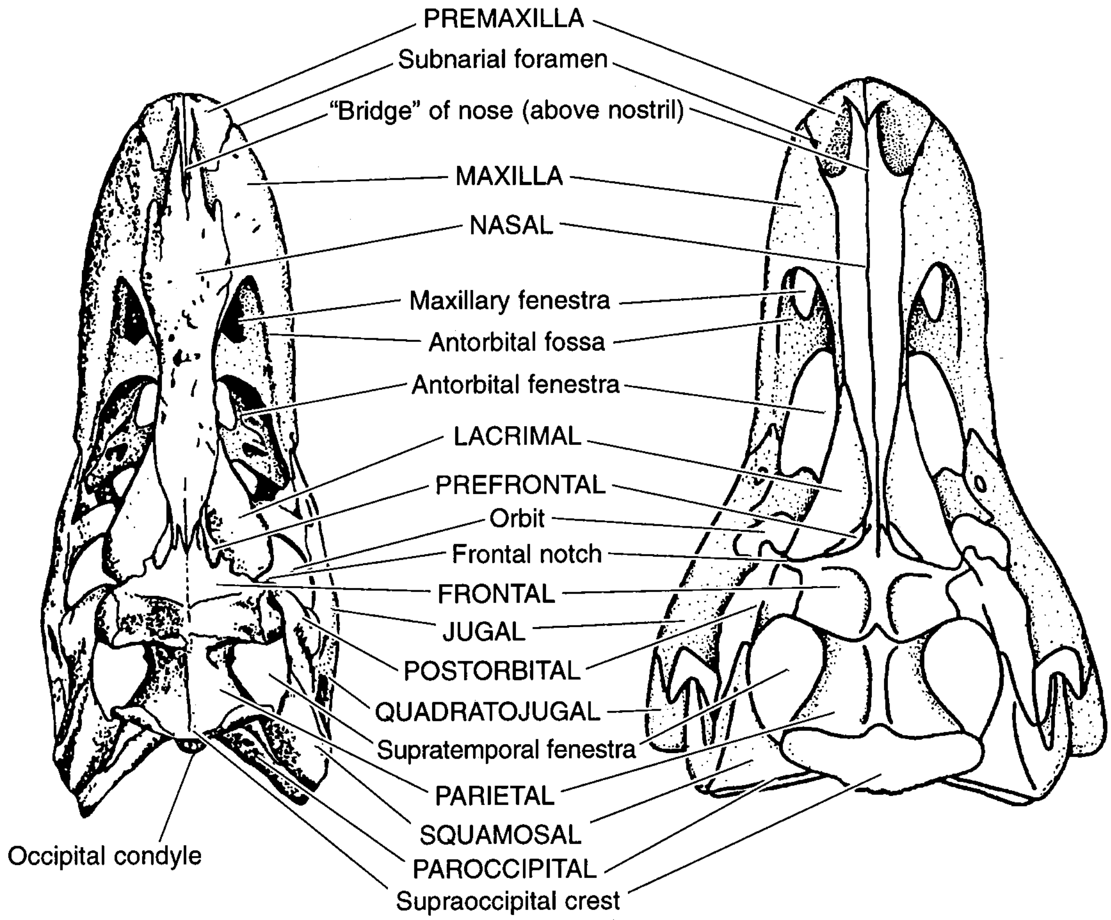


Figure 7.3. The skulls of the tyrant dinosaurs *Daspletosaurus torosus* (left) and *Tyrannosaurus rex* (right) in dorsal view, illustrating the important paired bones (in CAPITALS) and landmarks on the dorsal surface of the skull. Illustration by Tracy Ford.

In some dinosaurs with a horny beak, teeth in the premaxilla, and sometimes even in the maxilla, are absent. When a dinosaur, or a jawbone, has no teeth, it is said to be edentulous. In the ceratopsian (frilled or horned) dinosaurs, there is an additional bone anterior to the edentulous premaxilla. This bone is called the rostral (or "snout") bone. The rostral is a single bone, joining the two premaxillae.

In the rear of the skull, posterior to the orbit, lie additional openings in the skull. These are called the lateral temporal (or infratemporal) fenestra and the supratemporal fenestra. The lateral temporal fenestra is a large opening on the side of the skull, while the supratemporal fenestra is on the dorsal surface of the skull. Both are associated with the attachment of jaw muscles.

From these various landmarks, the positions of some of the other important skull bones can be determined (Figs. 7.2, 7.3). The jugal, or "cheekbone," is posterior to the maxilla and ventral to the orbit. The lacrimal is a small bone between the antorbital fenestra and the orbit. The quadrate is a major bone in the rear of the skull, where the cranium articulates with the mandible (lower jaw). All dinosaurs and birds have a quadrate/articular jaw joint; in other words, a bone in the back of the lower jaw bone, called the articular, articulates with the quadrate bone in the skull. (Mammals have a dentary/squamosal jaw joint, meaning that the bones forming the joint in mammalian jaws are not homologous to the bones forming the joint in dinosaurian jaws.)

A series of paired bones lie along the dorsal and posterior surface of the skull (Fig. 7.3). These bones meet along the midline, and so form "mirror images," right and left, of each other. The most anterior are the nasals, long paired bones on the dorsal surface of the skull, posterior to the premaxilla. Posterior to the nasals are the frontals. The parietals are paired bones above the braincase on the posterior surface of the skull, posterior to the frontal. The squamosals are on the posterior surface of the skull.

There are many bones which are joined together around the brain cavity. These tightly sutured bones are collectively called the braincase and lie inside the outer skull bones listed above. The spinal cord exits from the brain through the foramen magnum (or "great opening") on the posterior of the skull. Beneath the foramen magnum is a structure called the occipital condyle, a rounded knob joint (or condyle), where the cranium articulates with the vertebral column (Fig. 7.4). In humans, other mammals, and our extinct relatives, as well as in amphibians, there are two occipital condyles (one right, one left), but in dinosaurs and other reptiles there is only a single rounded knob directly ventral to the foramen magnum.

Teeth in dinosaurs share a similar overall structure in that they arise out of sockets in the dentary bone (lower jaw) and in the premaxilla and

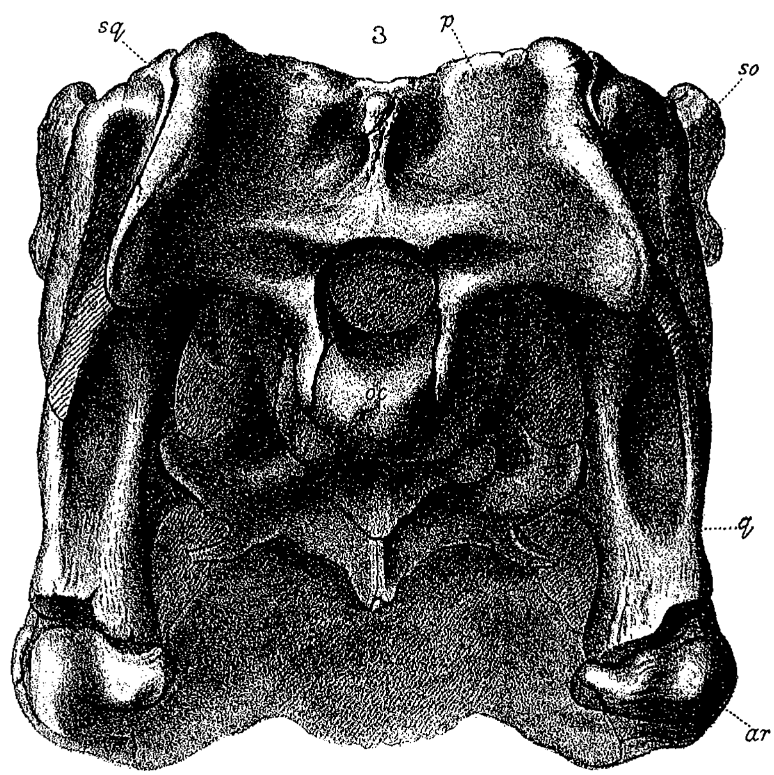


Figure 7.4. The skull of the armored dinosaur *Stegosaurus stenops* in posterior view, illustrating some important bones and landmarks of the rear of the skull. Illustration from Ostrom and McIntosh 1966. Original is a lithograph from a never-completed monograph on the Stegosauria to have been written by O. C. Marsh. Abbreviations: ar = articular; oc = occipital condyle; p = parietal; q = quadrate; sq = squamosal; so = supraorbial.

maxilla in the upper jaw. The teeth were ever-growing and ever-replacing, so that as one tooth was worn out (or ripped out), another grew out of the same socket to replace it. Dinosaurs had a continuing supply of teeth, unlike mammals, which get only two sets. In most dinosaurs (and in most other tetrapods), teeth were formed from a core of dentine and an outer surface of enamel. However, in two groups of herbivorous ornithischian dinosaurs (ornithopods and ceratopsians), the enameled surface was confined to one side of the tooth, and dentine formed only the surface of the other side. Because dentine is softer than enamel, the tooth became self-sharpening as the dentine wore away more quickly than the enamel when the teeth ground against each other. Dinosaur teeth did not really occlude against each other as they do in humans and most other mammals. Mostly they slid past each other in a slicing action. In ceratopsians the cutting surfaces of the teeth are oriented in a vertical plane that produces a scissors-like action. Because of their combination of slicing teeth and huge jaw muscles (ceratopsians may have had the strongest jaw muscles of any herbivorous animal), they have been called the "first Cuisinarts." Hadrosaurs are the only dinosaurs that "chewed" food, in that the teeth came together in a grinding action. Most saurischian dinosaurs simply grabbed food and swallowed it without the benefit of mastication.

In dinosaurs, as in most non-mammalian vertebrates, the mandible is composed of several different bones. The tooth-bearing bone of the mandible is called the dentary, and there are several bones posterior to it, which form the connection with the cranium. In mammals, the mandible is formed exclusively by the dentary. In the Ornithischia (bird-hipped dinosaurs), there is an extra bone in front of the dentaries. Called the predentary, this bone joins the two dentaries and forms a strong beak.

The Axial Skeleton

All the bones in the skeleton except for the skull are collectively referred to as the postcranium ("posterior to the cranium") (Fig. 7.5). The postcranium can be divided into two sections, often called the axial and appendicular skeletons. The axial skeleton is the "core" of an animal, its spine, trunk, and tail (the vertebrae). The appendicular skeleton refers to the fore- and hind limbs, and the girdles that attach the limbs to the trunk.

The most important part of the axial skeleton is the vertebral column. This column, the "backbone," is composed of many individual elements. Each of these bones is called a vertebra (plural *vertebrae*). A vertebra is composed of a large spool- or cylindrical-shaped structure, the centrum ("body," plural *centra*), ventrally, and a neural arch dorsally. On each neural arch are two sets of finger-like projections called the zygapophyses. Directed forward (angled upward and inward) are the prezygapophyses. These articulate with the postzygapophyses (facing backward and angled down and out) on the vertebra in front. These zygapophyses control the amount of movement between two vertebrae. Between the centrum and the neural arch runs the spinal cord. Projecting dorsally from the neural arch is a neural spine, to which are attached the back muscles (and which form the bumps down your spine).

The vertebral column of a dinosaur, like those of most non-mammalian tetrapods, is divided into four major segments (a mammalian column can be divided into five). These sections are the cervical (neck), dorsal (back), sacral (hip), and caudal (tail) vertebrae (Fig. 7.5). (In mammals, the dorsals can be divided into two separate segments: a thoracic, or chest, series, which has large ribs, and a lumbar, or lower back, series, in which there are no ribs.) The sacral vertebrae are often fused into a single structure in dinosaurs, called a sacrum (plural *sacra*). Dinosaurs are recognized as having three or more sacral vertebrae fused together (unlike most other reptiles, such as lizards and crocodiles, which have only two). The vertebrae of each of the different sections are shaped differently, reflecting the different requirements of the various sections of the body (i.e., flexibility in the neck, strength in the hips, etc.). Figure 7.6 illustrates a vertebra of the giant herbivorous dinosaur *Apatosaurus*.

The vertebrae of some dinosaurs are quite complex, with additional ridges, prongs, and other structures. One such structure is the hypantrum (a small anterior projection at the base of the neural spine), which articulates with the hyposphene (a small posterior projection at the base of the neural spine) of the preceding vertebra. Pleurocoels are openings along the lateral surfaces of vertebrae which open to a chamber inside the bone of the centrum and/or the neural arch. A pleurocoel can be a simple cavity, or it can be a very complex system of chambers and channels.

Lateral to the cervical and dorsal vertebrae are the ribs. Ribs (for some reason the only major part of the skeletal anatomy more commonly referred to by their English name than by their Latin name, costae) are long, narrow, paired bones forming a "cage" around the vital organs. The ribs of dinosaurs attach to the vertebrae at the bottom of the neural arch and the top of the centra by two separated projections. The ventralmost of these projections is the capitulum (plural *capitula;* "little head"), while the dorsalmost is the tuberculum (plural *tubercula;* "little lump"). Along the belly of some dinosaurs are gastralia (singular *gastralium*), or "belly ribs," which strengthened the ventral side of the animal and acted as a girdle to

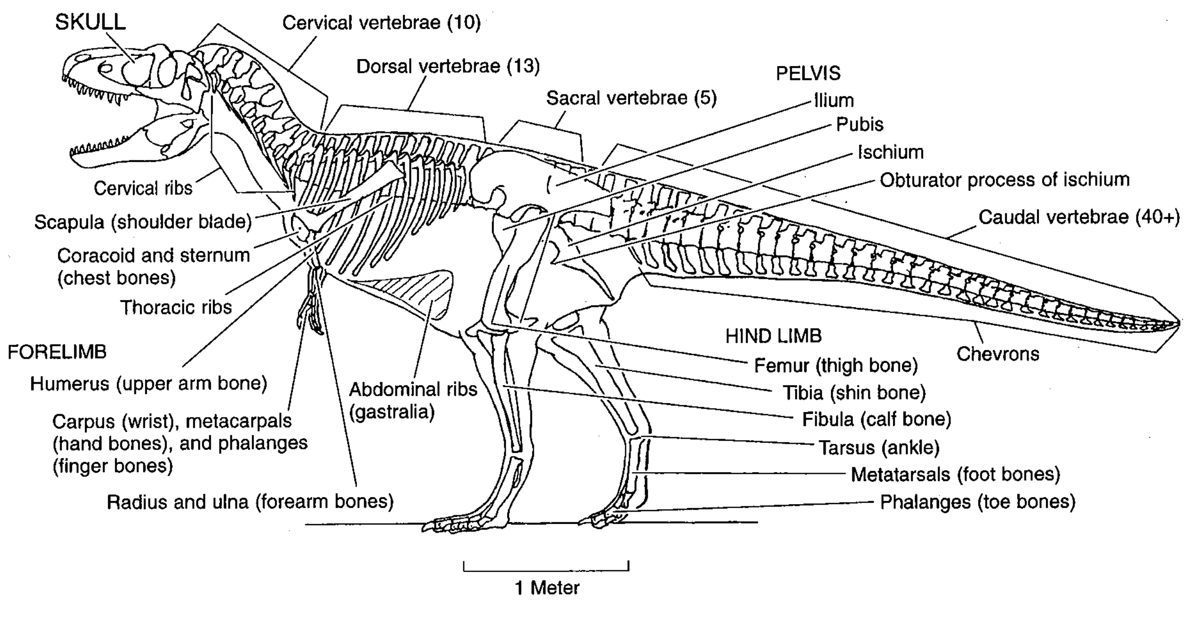


Figure 7.5. The skeleton of the tyrant dinosaur *Daspletosaurus torosus* in left lateral view, illustrating the postcranial skeleton. Illustration by Tracy Ford.

hold in the viscera ("guts"). Ventral to the caudal vertebrae are the chevrons, structures which are something like "tail ribs" or upside-down neural arches.

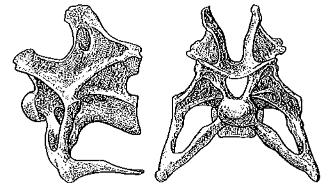


Figure 7.6. The 8th cervical (neck) vertebra of the gigantic sauropod dinosaur *Apatosaurus louisae,* in left lateral (*left*) and anterior (*right*) views. Illustration by Tracy Ford, modified from Gilmore 1936.

The Appendicular Skeleton

The appendicular skeleton refers to the fore- and hind limbs, and the girdles that attach these limbs to the body. Although there is a great similarity between the structures of the forelimb and the hind limb, the pattern of the girdles is very different.

The pectoral girdle attaches the forelimb to the trunk (Fig. 7.8). The largest of the bones in the pectoral girdle is the scapula (plural *scapulae*), or "shoulder blade." Ventral to the scapula is the coracoid. On the posterior surface of the girdle, the region where the scapula and coracoid meet forms a circular shoulder joint. In some dinosaurs, clavicles ("collarbones") are present, which attach the shoulder girdle to a series of fused bones along the ventral region of the chest. These fused bones formed the sternum (plural *sterna*), or "breastbone." In other, advanced, bird-like carnivorous dinosaurs there is a furcula ("wishbone," plural *furculae*) instead of clavicles. It is uncertain at present if furculae are formed by the fusion of the clavicles, or if they represent new structures (Bryant and Russell 1993).

Most of the forelimb, or arm, is made up of three bones. There is a single upper arm bone, the humerus (plural *humeri*), which joins the two forearm bones at the elbow. Of the two forearm bones, the ulna (plural *ulnae*) is the larger and more posterior, while the radius (plural *radii*) is generally smaller and more anterior. The many small bones of the wrist are known as the carpals. Distal to the carpals are the long bones of the palm of the hand, the metacarpals. The metacarpals are numbered in Roman numerals, from I to V, with I the most medial (inside, near the thumb) and V the most lateral (outside). The fingers are called digits, and they are numbered with the same scheme as the metacarpals (with digit I the "thumb" and digit V the "pinky"). The individual bones of the finger are called phalanges (singular *phalanx*). The distalmost of the phalanges are sometimes called the unguals, and supported the horny claws or hooves. Collectively, the digits, metacarpals, and carpals form the hand, or manus (plural *manus*).

The hind limbs attach to the axial skeleton at the pelvic girdle (Fig. 7.9). Also known as the pelvis ("hip," plural *pelves*), the pelvic girdle is

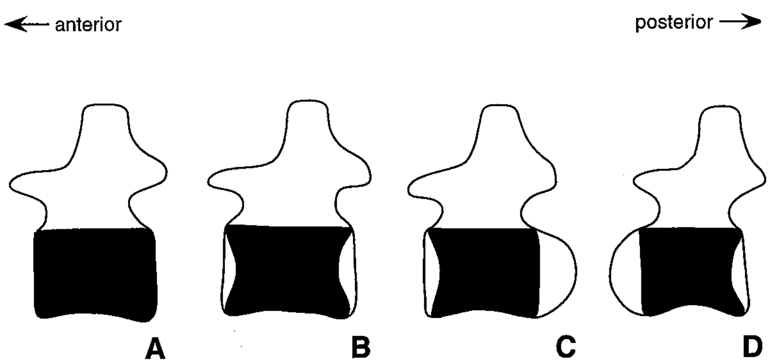


Figure 7.7. Schematic representation of the four main types of vertebral articulations. In each case the anterior end of the vertebra is to the left. (A) *amphiplatyan,* flat on both anterior and posterior ends; (B) *amphicoelous,* concave on both anterior and posterior ends; (C) *procoelous,* concave anterior end, strongly convex posterior end; (D) *opisthocoelous,* strongly convex anterior end, concave posterior end.

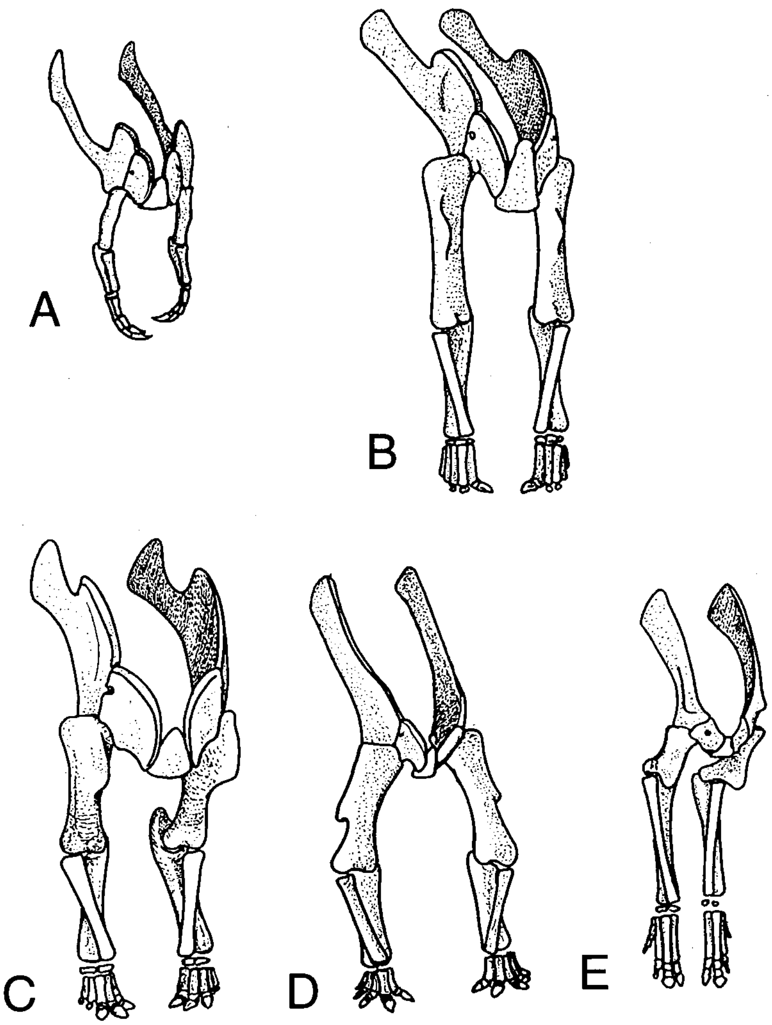


Figure 7.8. Forelimbs of the Dinosauria, in oblique right anterolateral view. (A) *Tyrannosaurus rex;* (B) *Apatosaurus louisae;* (C) *Stegosaurus stenops;* (D) *Chasmosaurus mariscalensis;* (E) *Corythosaurus casuarius.* Not to scale. Illustrations by Tracy Ford; modified from Osborn 1916, Gilmore 1936, Galton 1990, Lehman 1989, and Weishampel and Horner 1990.

composed of three bones per side. The largest of these is the ilium (plural *ilia*), which is the dorsalmost and which connects to the sacrum. Attaching beneath the ilium are the other two bones. The pubis (plural *pubes*) attaches anteriorly, and the ischium (plural *ischia*) attaches posteriorly. In most of the "lizard-hipped" or saurischian dinosaurs, the pubes point anteroventrally and the ischia posteroventrally (Figs. 7.9A–B). However, in the "bird-hipped" or ornithischian dinosaurs and certain "lizard-hipped" groups, the pubes point posteroventrally as well (Figs. 7.9C–E). Nevertheless, a pubis can always be distinguished from an ischium because the pubis attaches to the ilium anterior to the ischium. The ilium, pubis, and ischium form an open, round hole in the pelvis. Called the acetabulum (plural *acetabula*), this opening is the hip socket. In most tetrapods, including most mammals, turtles, lizards, and crocodiles, the acetabulum has a solid sheet of bone forming the medial wall of the socket. This condition is called a "closed" acetabulum. The Dinosauria, however, are specialized in having

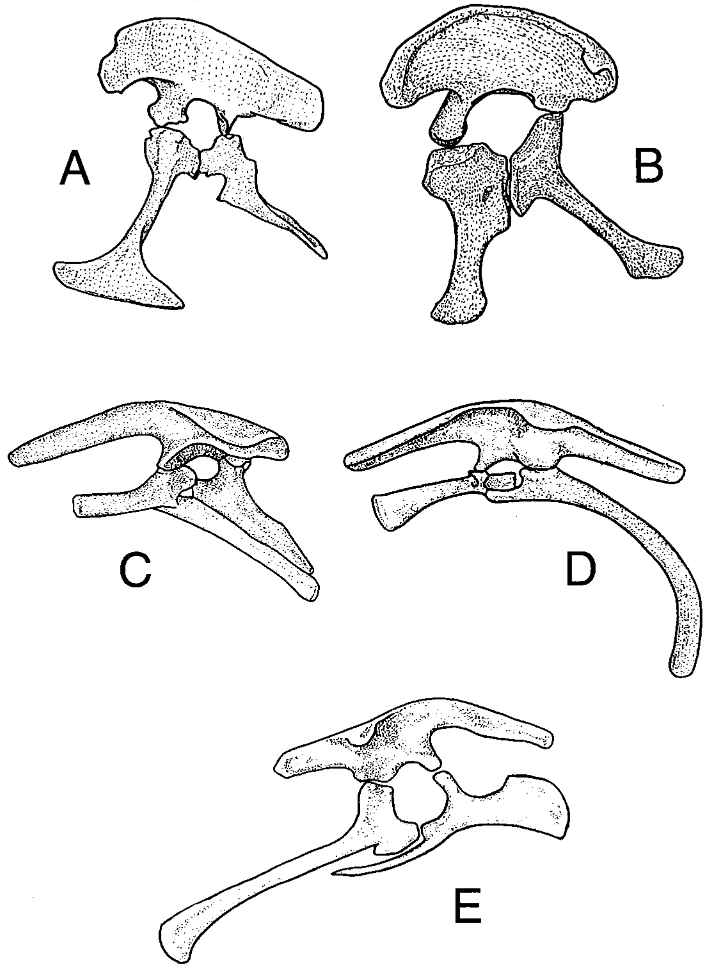


Figure 7.9. Pelvic girdles of the Dinosauria; A–D in left lateral view, E in right lateral view. Saurischian pelves: (A) *Tyrannosaurus rex;* (B) *Apatosaurus excelsus.* Ornithischian pelves: (C) *Stegosaurus stenops;* (D) *Chasmosaurus mariscalensis;* (E) *Corythosaurus casuarius.* Not to scale. Illustration by Tracy Ford.

an "open" acetabulum, one in which there was a hole all the way through the socket, and thus no medial wall of bone.

The pattern of bones in the hind limb, or leg, closely matches that of the forelimb (Fig. 7.10). There is a single upper leg, or thigh, bone, the femur (plural *femora*). The femur joins the lower leg at the knee, but there is no well-formed kneecap in the leg of a dinosaur. There are two bones in the lower leg: the tibia ("shin bone," plural *tibiae*), the larger and more medial of the two, and the fibula (plural *fibulae*), the thinner and more lateral one. Distal to the tibia and fibula are the tarsals, the small bones of the ankle. Unlike the complex ankle region of most tetrapods, the tarsals of dinosaurs are fairly simple. Two proximal elements, the larger, more medial astragalus (plural *astagali*) and the smaller, more lateral calcaneum (plural *calcanea*), adhere to the distal ends of the tibia and fibula, respectively. The other tarsals form a row of bones adhering to the long bones of the foot. There is no pronounced heel (posterior projection) in the ankle of dinosaurs, only a roller-joint between the astragalus/calcaneum and the distal tarsals. The long bones of the foot are called the metatarsals, numbered I to V in a medial-to-lateral fashion. Like the fingers, the toes are called digits,

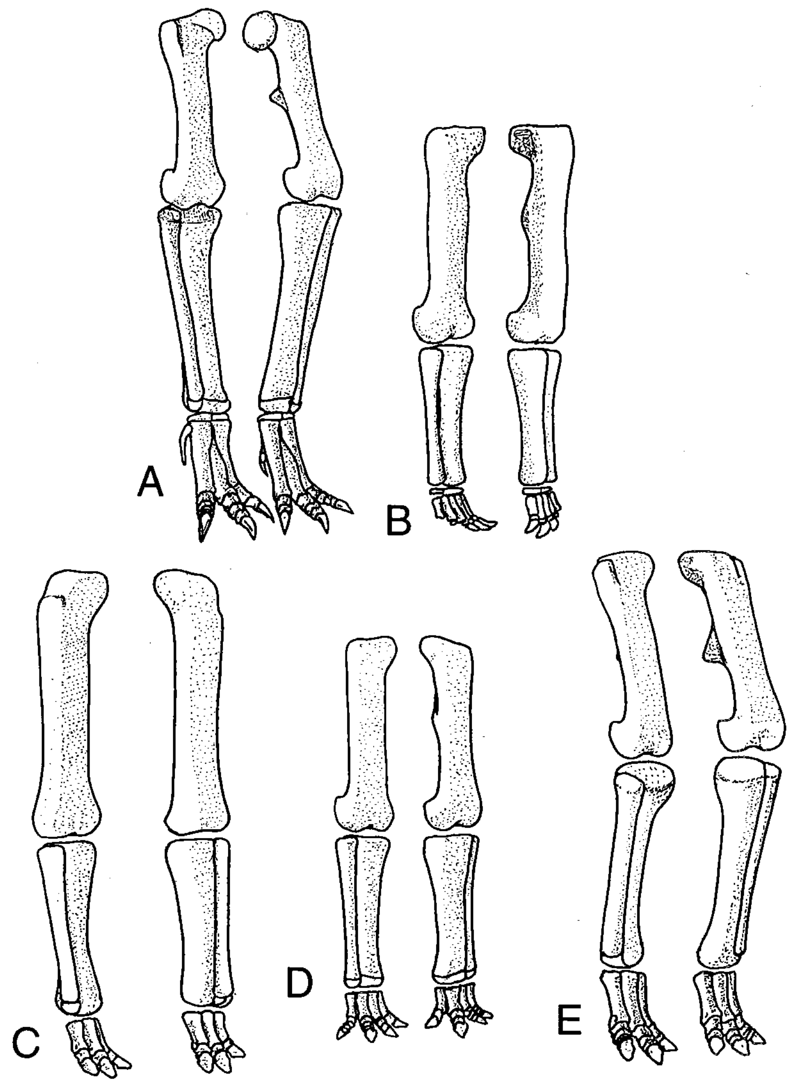


Figure 7.10. Hind limbs of the Dinosauria, in oblique right anterolateral view. (A) *Tyrannosaurus rex;* (B) *Apatosaurus louisae;* (C) *Stegosaurus stenops;* (D) *Chasmosaurus mariscalensis;* (E) *Corythosaurus casuarius.* Not to scale. Illustration by Tracy Ford.

numbered from the medialmost (I, the "big toe" in humans) to the lateralmost (V, the "little toe" in humans). Again as in the manus, each toe bone is a phalanx (plural *phalanges*), and the distalmost phalanges are unguals. The digits, metatarsals, and tarsals are collectively called the foot, or pes (plural *pedes*).

Unlike crocodiles, bears, and humans, which are plantigrade (flat-footed), dinosaurs are digitigrade. This means that dinosaurs walked on their toes, as chickens, cats, and dogs do. In order to distribute the weight of the animal, and act as a shock absorber, there was a pad of cartilage and connective tissues behind the foot. When you see the footprint of a large dinosaur, the front edges are marked by the bony claws, while the main depression is made by the non-bony pad.

Some dinosaurs also have a second set of bones in the body that arise out of the epidermis (outside skin). These bony growths, or osteoderms, form the many and varied patterns of armor seen in many dinosaurs. Most notable of these are the plates and spikes in stegosaurs and ankylosaurs. These were all anchored in the skin by connective tissue.

In order to strengthen the vertebrae in ornithischians, many of the tissues that connected the vertebrae together became filled with calcium and literally "turned to bone." These are the famous "ossified tendons" of the bird-hipped dinosaurs, and look somewhat like parallel strands of spaghetti. Those that occur below the tail and run across the chevrons between the caudal vertebrae are called hypaxial tendons. Those that occur above the vertebral centra and run across the neural spines are called epaxial tendons. In these dinosaurs, the base of the tail is very stiff, and not very mobile relative to the hips, while the tail becomes more mobile further posteriorly. In some saurischians (particularly some of the more advanced theropods), another path is followed. Instead of ossifying the tendons, the prezygapophyses of the vertebrae started to elongate and grow over several vertebrae at one time. In *Deinonychus,* these zygapophyses can cover as many as twelve vertebrae at one time. Similarly, the chevrons of *Deinonychus* were elongated to stiffen the tail. In dinosaurs such as this, the tail was most mobile anteriorly, and immobile distally, the opposite condition from what is found in ornithischians.

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