The Mesozoic extended for 186 million years, from the close of the Paleozoic 252 Ma to the beginning of the Cenozoic 66 Ma. Throughout this vast span of time, a worldwide fauna evolved, diversified, drifted with the moving continents, and radiated into most of the adaptive zones occupied by extant terrestrial vertebrates—and into some zones that no longer exist, such as those occupied by the enormous herbivorous and carnivorous tetrapods we call dinosaurs.

The Mesozoic saw the first modern vertebrate fauna, with all extant evolutionary lineages represented and with a full array of tetrapod herbivores and carnivores in the sea. Most of these animals were diapsids, the lineage that includes extant nonavian reptiles and birds. Mammals (synapsids), although present and diversifying, were a small part of the Mesozoic terrestrial fauna and, as far as we know, were absent from marine habitats.

19.1 Characteristics of Diapsids

The taxonomic categories Diapsida and Reptilia are confusing. The crown group Reptilia includes the common ancestor of all extant taxa of diapsids—that is, turtles, crocodylians, Birds, tuatara, and squamates (snakes and lizards). This chapter, however, focuses on extinct lineages of diapsids that are not among the groups encompassed by Reptilia, and thus we refer to these animals as diapsids rather than as reptiles.

The name diapsid means “two arches” and refers to the presence of an upper and a lower fenestra in the temporal region of the skull (Figure 19.1). More distinctive than the openings themselves are the bones forming the arches that border the openings. The upper temporal arch is composed of a three-pronged postorbital bone and a three-pronged squamosal. The jugal and quadra-togulal bones form the lower arch. The connection between the jugal and quadratojugal that forms the lower arch has been lost repeatedly in the radiation of diapsids, and the upper arch (postorbital-squamosal) has also been lost in some forms. Extant lizards and snakes clearly show the importance of those modifications of the skull in permitting increased skull kinesis during feeding, and the same significance may attach to the loss of the arches in some extinct forms.

Diapsids comprise two groups: Archosauromorpha (Greek archon, “ruler”; sauros, “lizard”; morphe, “form”) and Lepidosauromorpha (Greek lepisma, “scale”) (Figure 19.2). Lepidosauromorphs include Lepidosauria (rhynchocephalians, squamates, and their extinct relatives) as well as specialized marine tetrapods that are now extinct—the ichthyosaurs and sauropterygians.

Archosauromorphs include Testudines (turtles) and Archosauria (crocodylians, pterosaurs, nonavian dinosaurs, and birds). Two lineages of archosaurs are recognized, based on the articulation of the ankle joint. In Pseudosuchia, the ankle is a crurotarsal (crocodyloid) joint (see Chapter 14), meaning it can twist sideways as well as flex forward and backward; in Ornithodira, the ankle is a more rigid mesotarsal joint, with a straight-line hinge that can bend only forward and back (Figure 19.3).

Ecological relationships provide a perspective on Mesozoic diapsids (Table 19.1). Similar ecomorphs evolved in different lineages, and in some cases members of these lineages lived side by side and preyed on, or competed with one another.

19.2 Diversity of Mesozoic Diapsids

The end-Permian mass extinction described in Chapter 5 wiped out 70% of the terrestrial species of vertebrates (including synapsids, which had diversified in the Permian) and 95% of all marine species. Diapsids entered this nearly empty world and diversified into an enormous variety of animals, many of which were entirely different from anything that had preceded them.

- Marine diapsids (ichthyosaurs, placodonts, nothosaurs, pachypleurosaurs, plesiosauroids, and mosasaurs) first
**Figure 19.1** *Tyrannosaurus rex* illustrates the characters of the diapsid skull. Two temporal fenestrae are a distinguishing character of diapsids. In addition, archosaurs (crocodylians, pterosaurs, dinosaurs, and birds) have an antorbital fenestra on each side of the head, anterior to the eye, that houses an air sinus, and derived forms have a still more anterior maxillary fenestra. (EncycloPetey/CC BY-SA 3.0.)

**Figure 19.2** Phylogenetic relationships of Diapsida. Probable relationships among the major groups of diapsids; only the best-corroborated relationships are shown. Within archosauromorphs, turtles (Testudines) are the sister lineage of archosaurs. Within archosaurs, Pseudosuchia is the crocodile lineage (crocodylomorphs) and Ornithodira is the nonavian dinosaur and bird lineage. Three major lineages of lepidosauromorphs are distinguished. Ichthyosaurs and sauropterygians are extinct marine lineages that flourished during the Mesozoic. The lepidosaur lineage includes rhynchocephalians (diverse in the Mesozoic but with only one extant species, the tuatara) and squamates (lizards and snakes, with more than 10,000 extant species).
appeared in the Triassic and diversified into the adaptive zones now occupied by sharks, seals, sea lions, walruses, and toothed whales, as well as some groups that have no extant parallels.

- On land, *crocodylomorphs* and several lineages of basal archosaurs were the earliest diapsid lineages to diversify as predators. Crocodylomorphs continued to diversify through the Mesozoic and into the Cenozoic. In the Southern Hemisphere, crocodylomorphs appear to have remained more abundant and diverse than dinosaurs, at least into the Early Cretaceous.

- Flying diapsids evolved twice—pterosaurs in the Late Triassic, followed by birds in the Jurassic. The two groups were contemporaneous from the Jurassic through the Cretaceous, a span of about 100 million years.

- The earliest dinosaurs appeared in the Middle Triassic, but dinosaurs were not very diverse until the Jurassic. The diversification of dinosaurs appears to have progressed in three stages. Their initial appearance 235–228 Ma was followed by a major radiation in the Middle to Late Jurassic (174–164 Ma) and then several pulses of diversification during the Cretaceous.

### Table 19.1 Ecological Diversity of Mesozoic Diapsids

<table>
<thead>
<tr>
<th>Group</th>
<th>Habitat</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>LEPIDOSAUROMORPHA</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ichthyosaurs</td>
<td>Marine</td>
<td>Predators with body forms resembling those of sharks and cetaceans</td>
</tr>
<tr>
<td>Placodonts</td>
<td>Marine</td>
<td>Coastal herbivores</td>
</tr>
<tr>
<td>Pachypleurosaurs</td>
<td>Marine</td>
<td>Small predators</td>
</tr>
<tr>
<td>Nothosaurs</td>
<td>Marine</td>
<td>Medium-size predators</td>
</tr>
<tr>
<td>Plesiosaurs</td>
<td>Marine</td>
<td>Two types of large predators: long-necked plesiosaur and short-necked pliosaurs</td>
</tr>
<tr>
<td>Mosasaurs</td>
<td>Marine</td>
<td>Predators related to extant varanid lizards</td>
</tr>
<tr>
<td>Rhynchocephalians</td>
<td>Terrestrial</td>
<td>Small to medium-size herbivores</td>
</tr>
<tr>
<td><strong>ARCHOSAUROMORPHA</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Turtles</td>
<td>Terrestrial, semi-aquatic, and marine</td>
<td>Carnivores and herbivores (see Chapter 16)</td>
</tr>
<tr>
<td>Crocodylomorphs: Metriorhynchids</td>
<td>Marine</td>
<td>Coastal predators related to crocodyliforms</td>
</tr>
<tr>
<td>Crocodylomorphs: Crocodyliforms</td>
<td>Semi-aquatic to terrestrial</td>
<td>Small herbivores and small to enormous carnivores (see Chapter 18)</td>
</tr>
<tr>
<td>Basal archosaurs (Rhynchosaurs)</td>
<td>Terrestrial</td>
<td>Herbivores</td>
</tr>
<tr>
<td>Ornithischian dinosaurs</td>
<td>Terrestrial</td>
<td>Herbivores</td>
</tr>
<tr>
<td>Saurischian dinosaurs: Sauropods</td>
<td>Terrestrial</td>
<td>Herbivores</td>
</tr>
<tr>
<td>Saurischian dinosaurs: Theropods</td>
<td>Terrestrial</td>
<td>Carnivores and omnivores</td>
</tr>
<tr>
<td>Pterosaurs</td>
<td>Aerial; secondarily terrestrial and aquatic</td>
<td>Filter feeders, predators, scavengers, mollusk-eaters, and omnivores</td>
</tr>
<tr>
<td>Birds</td>
<td>Aerial; secondarily terrestrial and aquatic</td>
<td>Small to very large carnivores, omnivores, and herbivores (see Chapters 21 and 22)</td>
</tr>
</tbody>
</table>
19.3 Lepidosauromorphs: Marine Diapsids

Extant lepidosaurs (lizards, snakes, and the tuatara) are terrestrial, but during the Mesozoic lepidosauromorphs dominated the seas.

**Terrestrial lepidosauromorphs**

Rhynchocephalia (Greek *rhynchos*, “beak”; *kephale*, “head”) was the only lineage of lepidosauromorphs that radiated extensively on land. Triassic rhynchocephalians were small (15–35 cm), light-bodied insectivores with small conical teeth. These early rhynchocephalians were lizardlike in body form and probably in ecology as well. Rhynchocephalians from the Jurassic and Early Cretaceous were up to 1.5 m long, and variation in their teeth indicates that they had radiated into new feeding niches: there were bladelike teeth for cutting and slashing, long pointed teeth for capturing fish, broad teeth for crushing armored prey, grinding teeth for shredding plants, and a remarkable species with jaws lined by massive, continuously growing tooth plates.

Although the tuatara is a member of an ancient lineage, the genus *Sphenodon* is no more than 100,000 years old. Except for reestablishment of a complete lower temporal arch, the tuatara is morphologically similar to some Mesozoic rhynchocephalians, but at the molecular level the tuatara has the highest rate of evolution known among vertebrates.

Lizards and snakes radiated during the Mesozoic, and some snakes grew large enough to prey on dinosaur eggs and hatchlings, but these lineages have reached their greatest diversity in the Cenozoic.

**Marine lepidosauromorphs**

Lepidosauromorphs were well represented in the complex marine ecosystems of the Early Triassic and included coastal herbivores as well as both coastal and pelagic predators.

**Ichthyosaurs**  Ichthyosaurs probably are the most familiar of the Mesozoic aquatic diapsids. Basal ichthyosaurs retained the lizardlike body form of their terrestrial ancestors, but the derived ichthyosaurs that lived during the Jurassic were more streamlined (Figure 19.4A,B). Ichthyosaurs had a hypocercal tail with the vertebral column bending sharply downward into the ventral lobe of the caudal fin. The upper lobe was formed of stiff tissue, and the lobes were nearly symmetrical. Ichthyosaurs also had a dorsal fin that was supported only by stiff tissue, not by a bony skeleton, and the paddles were extended by skin and connective tissue. We know about these soft tissues because ichthyosaur fossils in fine-grained sediments near Holzmaden in southern Germany contain an outline of the entire body preserved as a carbonaceous film.

Ichthyosaurs had both forelimbs and hindlimbs, unlike extant cetaceans (whales and porpoises), which retain only the forelimbs. The limbs of ichthyosaurs were modified into paddles by both *hyperdactyly* (addition of extra fingers and toes) and *hyperphalangy* (addition of extra bones lengthening the fingers and toes).

The streamlining of later forms may have been associated with the development of carangiform locomotion (see Chapter 8) and rapid pursuit of prey. The Jurassic was the high point of ichthyosaur diversity. Ichthyosaurs were less abundant in the Early Cretaceous, and only a single family remained by the Late Cretaceous. Ichthyosaurs disappeared 30 million years before the end-Cretaceous extinction, perhaps victims of the global warming that characterized the Late Cretaceous.

Fossil ichthyosaurs with embryos in the body cavity indicate that these animals were viviparous. Some fossils may be those of females that died in the process of giving birth, as they preserve the young emerging tail-first, as in extant cetaceans and sirenians (manatees and sea cows). The terrestrial ancestors of ichthyosaurs appear to have been viviparous, but tail-first birth is a derived character associated with marine life.

Most ichthyosaurs had large heads with long, pointed jaws that were armed with sharp teeth. Stomach contents preserved in some ichthyosaur specimens include cephalopods and fishes, and the remains of a hatchling sea turtle and a bird have been found in fossil ichthyosaurs from the Cretaceous. The aptly named *Thalattoarchon saurophagus* (Greek *thallasa*, “sea”; *archon*, “ruler”; *phago*, “eat”) was nearly 9 m long with a skull estimated to have been more than 1.2 m

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1 Two lineages of diapsids with beaklike snouts have confusingly similar names. Rhynchocephalia ("beak heads," with one extant species, the tuatara) are lepidosauromorphs, whereas the extinct Rhynchosauria ("beak lizards") were archosauromorphs.
long and with bladelike teeth with serrations on both edges, and was an apex predator during the Middle Triassic.

Species of the Triassic genus *Shastasaurus* had short snouts and were toothless; they lacked the characters of the hyobranchial apparatus that characterizes suction feeders. Instead, they may have been ram-feeders, engulfing prey by swimming over it.

Derived ichthyosaurs had very large eyeballs that were supported by a ring of sclerotic bones. A *Temnodontosaurus* 9 m long had an eyeball with a diameter of 253 mm—roughly equivalent to an eye diameter of 50 mm for a human. These ichthyosaurs are believed to have hunted at great depths—500 m or more—and to have detected light emitted by the photophores of their prey. Traces of melanin in the skin of these deep-diving ichthyosaurs suggest that they were a uniform dark color, without the countershading (dark dorsal surface, light ventral surface) that is characteristic of most aquatic vertebrates.

**Placodonts**

The Triassic placodonts were the least specialized of the marine lepidosauromorphs, retaining many characteristics of their terrestrial ancestors. They lived in shallow water habitats in the Tethys Sea (the body of water that spread from east to west as Laurasia and Gondwana separated during the Mesozoic). Basal forms, such as *Placodus*, were stocky with short legs and land feet modified as paddles. The tail was not laterally flattened and was probably not used in swimming. Broadened gastralia (bones in the ventral abdominal wall; see Chapter 14) covered the ventral surface of placodonts, and the dorsal surface of some species was covered by polygonal bony plates (Figure 19.5).

**Nothosaurs and pachypleurosaurs**

Nothosaurs (0.2–1 m) and pachypleurosaurs (1–4 m) were elongated marine predators with laterally flattened tails and slender jaws armed with short, pointed teeth. These characters suggest that nothosaurs and pachypleurosaurs were pursuit predators, akin to modern-day long-snouted dolphins, that chased and captured fish.

**Plesiosauroids**

Plesiosauroids appeared in the Late Triassic and persisted to the very end of the Cretaceous. Basal forms had slightly elongated necks, with heads were proportional to their body size. Two ecological specializations—pliosaurs and plesiosaurs—were represented among derived plesiosauroids. Pliosaurs had long skulls (more than 3 m in some forms) and short necks (about 13 cervical vertebrae), whereas plesiosaurs had small skulls and exceedingly long necks with 32–76 vertebrae (Figure 19.6). The necks of plesiosaurs could bend downward, but not readily upward or to the side.

Both types of plesiosauroids had heavy, rigid trunks and appear to have rowed through the water with limbs that acted like oars and may also have served as hydrofoils, increasing the efficiency of swimming. Hyperphalangy increased the size of the paddles, and some plesiosaurs had as many as 17 phalanges per digit. In both types of plesiosauroids, the nostrils were located high on the head just in front of the eyes.

Pliosaurs developed an increasingly streamlined body form during their evolution as the neck became shorter and the paddles larger, whereas plesiosaurs became less...
streamlined as their necks lengthened and the paddles became smaller in proportion to body size. Pliosaurs were probably speedy swimmers that might have captured swimming cephalopod mollusks and fish by pursuing them the way seals and sea lions hunt their prey; the large species may have preyed on other marine diapsids. The downward-bending neck suggests that plesiosaurs may have fed on bottom-dwelling prey.

Plesiosauroids were viviparous. A fossil of the Late Cretaceous plesiosaur *Polycotylus latippinus* contains a single embryo, not yet at full term but already 32% of the body length of its mother. That is remarkably large, and the embryo’s probable size at birth, based on the extent of ossification, was 35–50% of its mother’s length. Other marine diapsids were viviparous, but those species produced litters consisting of several juveniles, each only 15–30% of the mother’s body length. Production of a single, large offspring appears to have been unique to plesiosaurs among Mesozoic diapsids.

**Mosasaurs** Mosasaurs were a Late Cretaceous radiation of varanid lizards into the shallow epicontinental seas that spread across North America and Europe at that time. Early mosasaurs, such as *Aigialosaurus dalmaticus* from Texas, had body proportions like those of modern varanid lizards, and their limbs ended in digits (Figure 19.7A). They probably swam with lateral undulations of the body and tail. The limbs of more derived mosasaurs had elongated digits connected by webbing that converted them into paddles, but their limbs were small and probably played little role in locomotion, unlike the much larger paddles of plesiosaurs. The most derived mosasaurs, including *Tylosaurus poriger*, had a hypocercal tail (Figure 19.7B). These forms probably used a modified carangiform swimming mode and would have been faster than the earlier forms.

The earliest mosasaurs were about 1 m long, but they increased in size during their evolutionary history, and the largest species reached lengths of 17 m or more. Examination of their teeth suggests that mosasaurs had radiated into a variety of adaptive zones. Their skulls were highly kinetic, an ancestral feature of varanid lizards, and the teeth of most species were sharp and conical—effective for seizing and holding prey. Mosasaurs probably ate whatever they were able to catch, and we know something of their diets from fossils that were preserved with the animals’ last meals still intact. A single specimen contains bones from a fish, a smaller mosasaur, a flightless seabird, and possibly a shark. A turtle and a plesiosaur have been found in the stomachs of other mosasaurs. Fossil shells of ammonites (pelagic cephalopod mollusks) with marks that appear to match the shape and arrangement of mosasaur teeth have...
been described, and a fossil of Globidens, a specialized mosasaur with massive blunt teeth, has the remains of clam shells in its abdomen.

Mosasaurs were viviparous, giving birth to litters of four or five young, each about 15% of the body length of the mother. A fossil of Carosaurus marchesi, a mid-Cretaceous mosasaur, contains at least four advanced embryos. The orientation of the embryos suggests that they were born tail-first, like ichthyosaurs and extant cetaceans and sirenians, reducing the risk that the babies would drown before they had fully emerged.

19.4 Metriorhynchid Crocodylomorphs

Metriorhynchid crocodylomorphs constituted the only successful marine radiation by archosaurs during the Mesozoic. Metriorhynchids appeared in the Early Jurassic and persisted through the Early Cretaceous. Even the basal members of the group displayed a suite of adaptations to marine life, and the derived forms that lived in the Cretaceous were highly specialized (Figure 19.8). Their heads were streamlined, and air spaces in the bones made their skulls light, probably allowing them to float at the surface with only their heads protruding. The limbs of metriorhynchids were paddlelike, and the posteriormost vertebrae turned sharply downward to create a hypocercal tail with an upper lobe supported by only stiff tissues, as in derived ichthyosaurs and mosasaurs.

Most metriorhynchids were probably fish eaters, but species in the Cretaceous genera Dakosaurus and Geosaurus were probably apex predators that could attack and kill prey larger than themselves. Dakosaurus had bone-crunching jaws that could exert enormous force, whereas the teeth in the upper and lower jaws of Geosaurus formed a pair of blades that could slice through tissue. In addition, species in both genera probably employed the crocodylian death roll—seizing prey and then rotating rapidly around their own long axis, twisting off portions of the prey.

19.5 Pterosaurs: The First Flying Vertebrates

Archosaurs gave rise to two independent radiations of fliers: pterosaurs and birds. Pterosaurs first appeared in the Late Triassic, some 80 million years before the earliest birds. Pterosaurs persisted until the end of the Cretaceous and diversified into the major adaptive zones occupied by extant birds (Figure 19.9).

“Rhamphorhynchoids” were basal pterosaurs (probably a paraphyletic grouping) that retained a long tail stiffened by bony projections extending anteriorly, overlapping half a dozen vertebrae and preventing the tail from bending horizontally or dorsoventrally. A leaf-shaped expansion at the end of the tail may have acted as a rudder. Derived (ptero-
dactyloid) pterosaurs, which were larger than rhamphorhynchoids and lacked tails and teeth, appeared in the Middle Jurassic and persisted until the end of the Cretaceous.

The structure of pterosaurs

The mechanical demands of flight are reflected in the structure of flying vertebrates, and it is not surprising that pterosaurs and birds show a high degree of convergent evolution. In derived pterosaurs, the teeth were reduced or entirely absent; the tail was lost; the sternum developed a keel that was the origin of flight muscles; the thoracic vertebrae became fused into a rigid structure; the bones were thin-walled; postcranial pneumatization (the development of open spaces in bone) was extensive; and the eyes, the parts of the brain associated with vision, and the cerebellum (which is concerned with balance) were large while the olfactory areas were small. Pterosaurs probably had a unidirectional flow of air through the lungs.

Limbs and locomotion The limbs of pterosaurs were large in relation to the trunk and abdomen. The wings were formed by skin stiffened by internal fibers and were entirely different from the feathered wings of birds. The primary wing of pterosaurs, the brachiopatagium (arm wing), was supported anteriorly by the upper and lower arm bones and an extremely elongated fourth finger. A small splintlike bone, the pteroid, was attached to the front edge of the fourth finger and may have supported a membrane that ran forward to the neck. The brachiopatagium extended posteriorly to the hindlegs.

A posterior wing, the uropatagium (tail wing), provided additional lift at the rear of the body. The uropatagium of rhamphorhynchoid pterosaurs extended between the hindlegs, limiting their capacity for independent movement. In pterodactyloids, the uropatagium was reduced, extending from the pelvis to the ankle of each leg and allowing the hindlimbs to move independently.

Figure 19.8 Metriorhynchids were marine crocodylomorphs. (A) Geosaurus, from the Cretaceous, had a short snout, suggesting that it fed on other large marine reptiles rather than on fish. (B) The slender snout of Metriorhynchus superciliosus, a Late Jurassic species, suggests that it fed on fish. Both species were about 3 m long. (A, Dmitry Bogdanov/CC BY 2.5; B, Dmitry Bogdanov/CC BY 3.0.)
Pterosaurs walked quadrupedally (Figure 19.10). The uropatagium of rhamphorhynchoids probably required them to move the hindlegs together in a hopping gait, but pterodactyloids were able to stride. Trackways of walking pterodactyloids have been found in Jurassic and Cretaceous sediments on most continents. No tracks of ramphorhynchoids have been discovered, and basal pterosaurs may have climbed on trees and cliffs instead of walking across flat surfaces.

Aerodynamic tests and modeling indicate that all pterosaurs could fly, despite the fact that the largest species had wingspans of 10 m and weighed 200 kg or more. The long, narrow wings of large species of pterosaurs were similar to those of birds such as albatrosses that glide at high speeds for great distances. The smallest pterosaur, the pterodactyloid *Nemicolopterus crypticus*, was a forest-dweller with a wingspan of only 25 cm. It probably had short, broad wings like those of birds that fly through woodlands.

How a pterosaur took flight has long been a subject of debate. Through most of the 20th century, reconstructions of pterosaurs showed them posed on cliffs, reflecting a belief that launching from a height was the only way a pterosaur could get into the air. More recently, a bipedal running takeoff was proposed, but both mechanical and aerodynamic arguments have discredited that hypothesis. The most likely method is a quadrupedal leap, which would have allowed the wing and hindlimb muscles to act simultaneously to produce high launch speeds and
in the Jurassic and Cretaceous that combined long jaws with extremely long, closely set teeth are believed to have been filter feeders. Dsungaripterids had long, narrow jaws with no anterior teeth; they may have used a pincerlike motion to pluck mollusks from rocks at low tide, then crushed them with broad, flat teeth at the rear of the jaws. Tapejarids had deep skulls with toothless beaks and may have been frugivorous, while istiodactylids had broad snouts with interlocking lancet-shaped teeth and were probably scavengers.

Azhdarchids (Uzbek *azhdarkho*, “a mythical dragon”) may have been the most remarkable pterosaurs. Most species in this Cretaceous lineage of derived pterydactyloids were very large; *Arambourgiania philadelphiae* could have stood eye-to-eye with a giraffe (Figure 19.11).

Azhdarchids were terrestrial stalkers that foraged quadrupedally, using their long necks and beaks to seize prey. Described relatively recently, azhdarchids are turning out to be more diverse than was originally realized. The smallest species yet discovered was about the size of a house cat and had a wingspan of about 1.5 m, whereas the heads of the largest species were 4 m above the ground when they stood erect, and their wingspans were 10–11 m. Azhdarchids have no extant analogues, but in behavior and ecology they probably resembled ground hornbills and marabou storks, except that they were much larger than the birds.

Two general types of giant azhdarchids have been distinguished: gracile and robust. *Arambourgiania philadelphiae* is representative of gracile azhdarchids, which had long necks and relatively light skulls. *Hatzegopteryx thambema*, a robust form, had a shorter neck than *A. philadelphiae* but a larger, heavier bill. *A. philadelphiae* may have preyed on relatively small animals—up to the size of a human—whereas *H. thambema* was probably an apex predator, capable of killing dinosaurs. Indeed, it may be significant that fossils of large predatory dinosaurs have not been found in the deposits that contain azhdarchid pterosaurs.

**Body covering and crests** Fossils of *Sordes pilosus* and *Jeholopterus ningchengensis* from fine-grained sediments show that their skin was covered by fine, hairlike fuzz called *pycnofibers* that probably provided insulation. A fuzzy body covering was probably widespread among pterosaurs; in addition to providing insulation, pycnofibers were probably colorful, forming patterns used for species and sex recognition.

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**Figure 19.10** Pterosaurs walked quadrupedally. A reconstruction of a walking *Pterodactylus* shows the erect stance and limb movement of a pterodactyloid pterosaur. Only the first three fingers of the forefeet touched the ground; the long fourth finger that supported the brachio-patagium was apparently folded against the body. The wrist was rotated outward, so impressions of the fingers of the forefoot are directed to the side and backward. The toes and soles of the hindfeet were in contact with the ground. (Copyright © Mark Witton.)

**Figure 19.11** The largest azhdarchid pterosaurs were apex predators. *Arambourgiania philadelphiae* (center) could have confronted an adult giraffe eye-to-eye. *Hatzegopteryx thambema* (right) was not quite as tall as *A. philadelphiae*, but it was more robust. Both of these pterosaurs were large enough to have preyed on animals the size of humans, and *H. thambema* may have preyed on dinosaurs. (Copyright © Mark Witton.)
Many pterosaurs had crests on their heads. These crests appeared early in the evolution of pterosaurs and included an enormous variety of sizes and shapes. Crests were formed by bones alone, by bones with soft tissue, or by soft tissue alone. The crests grew allometrically, becoming larger as an individual matured, and in many species they were sexually dimorphic—large in males and small or absent in females. Both of these characteristics suggest that the crests were used during intraspecific interactions, such as courtship and territorial disputes. Tests with models of pterosaurs in wind tunnels indicate that even large crests had little aerodynamic effect.

**Reproduction, eggs, and parental care**

Pterosaurs were oviparous, like all other archosaurs, but their eggs had flexible shells like those of many squamates, instead of the rigid shells that characterize the eggs of crocodilians, nonavian dinosaurs, and birds. The eggs were small in relation to the size of the adults. Pterosaurs appear to have hatched at an advanced stage of development and, like some species of brush turkeys (megapode birds; see Chapter 22), were probably able to run and fly soon after emerging from the nest.

**Did the evolution of birds doom the pterosaurs?**

Pterosaurs had diversified widely by the Late Jurassic when the first birds appeared, and they filled a large number of adaptive zones that appear to be occupied now by birds. Thus, it is tempting to propose that competition with birds drove pterosaurs to extinction, but available evidence does not clearly support that hypothesis. A comparison of the body forms of pterosaurs and birds indicates that they occupied statistically different morphospaces—that is, they had different combinations of anatomical features, and as a result they did not overlap in the ways they lived. Thus, this analysis does not support the hypothesis of competition between pterosaurs and birds.

However, the appearance of birds coincided with an increase in the wingspan of pterosaurs from an average of about 1.5 m to about 7 m, while the wingspans of birds decreased to between 10 cm and 1 m. Character displacement of that sort might result from competition, but the timing of the increase in body size of pterosaurs also corresponds to the appearance of pterodactyloids and the gradual disappearance of ‘thamphorhynchoids.”

If competitive replacement did occur, it was remarkably slow. Birds appeared in the Late Jurassic, and pterosaurs persisted until the end of the Cretaceous; thus, they lived side by side for nearly 100 million years.

**19.6 Triassic Faunal Turnover**

Although dinosaurs are the iconic organisms of the Mesozoic, they appeared only in the Middle Triassic and did not begin to diversify until the Late Triassic and Early Jurassic.

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**Figure 19.12 Three diapsid faunas radiated during the Triassic.** From the Middle Permian to the Middle Triassic, carnivorous and herbivorous synapsids were the most abundant tetrapods in terrestrial habitats. In the Early Triassic synapsids achieved a worldwide distribution of rabbit- to cow-size herbivores (dicyodonts, traversodontids) that were preyed on by fox- to lion-size carnivores (cynodonts). Dipsads replaced synapsids as the most diverse and abundant terrestrial amniotes in the Early and Middle Triassic. Rhychosaurs were the first diapsids to radiate. Initially a minor component of terrestrial faunas, rhychosaurs replaced synapsids as the most abundant herbivores in the Middle to Late Triassic. A variety of pseudosuchians composed the major assemblage of carnivores, and the heavily armored aetosaurs were the first herbivorous archosaurs. Ornithodirans displaced pseudosuchians during the Middle and Late Triassic. The first dinosauromorphs appeared early in the Middle Triassic and diversified during the Triassic turnover, when climates shifted from damp to arid. By the Late Triassic, dinosauromorphs had replaced synapsids and rhychosaurs as the most abundant herbivores. Carnivorous dinosaurs (theropods) were diverse and abundant in the Late Triassic. The end-Triassic mass extinction wiped out all pseudosuchians except for crocodylians, and the Jurassic saw a major expansion of herbivorous and carnivorous dinosaurs. (Modified from Benton et al. 2014.)

Two earlier radiations preceded the appearance of dinosaurs (Figure 19.12):

- From the Middle Permian to the Middle Triassic, synapsids were the most abundant tetrapods in terrestrial habitats. Cynodonts were carnivores that ranged from the size of foxes to wolves. Several lineages, including dicynodonts and traversodontids, were herbivores, ranging in size from a few kilograms to as much as 600 kg. Most of these lineages were extinct by the Late Triassic.
- Rhychosaurs, basal archosauromorphs, were small herbivores in the Early Triassic, but by the Middle Triassic some species were up to 2 m long. They fed on tough vegetation with a shearing dentition and jaw action. During the Middle Triassic, basal pseudosuchians diversified into predators (ornithosuchids, rauisuchians, and phytosaurs) and herbivores (aetosaurs). Herbivorous lineages of dinosaurs began to diversify in the Late Triassic. Initially the herbivorous sauropodomorph dinosaurs expanded, replacing herbivorous synapsids, aetosaurs, and rhychosaurs. Carnivorous lineages of dinosaurs did not diversify until after phytosaurs, ornithosuchids, and rauisuchians disappeared during the end-Triassic mass extinction. Several lineages of basal ornithodirans radiated in the Triassic. These animals can be described as “almost dinosaurs” because they had some, but not all, of the derived characters of dinosaurs. Our understanding of relationships among these lineages and of these lineages to dinosaurs (Dinosauria) is in flux as new fossils are discovered and older specimens are reanalyzed. The basal lineages were diverse in body form and ecology: *Marasuchus lilloensis* was a bipedal carnivore, only 30–40 cm long; *Sacisaurus agudoensis*, *Silesaurus opolensis*, and *Asilisaurus kongwe* were lightly built quadrupedal omnivores or herbivores, 1.5–2.5 m long.
When most people hear the word "dinosaur," the image that comes to mind is a large animal—either a fearsome predator like *Tyrannosaurus rex* or an enormous, long-necked herbivore like *Apatosaurus*. However, the diversity of sizes and body forms of nonavian dinosaurs extends far beyond those two examples. The huge species were indeed spectacular, but there were also dinosaurs that were about the size of a chicken. In addition, traditional reconstructions of dinosaurs as a uniform gray or tan are probably also incorrect. Species that relied on camouflage to avoid detection by predators probably had colors and patterns that obscured their outlines, and it is likely that many feathered dinosaurs were as flamboyant and colorful as birds are today.

Mobility and social interaction were important components of the biology of many dinosaurs. Their mobility owed much to the structure of their hindlimbs, and their social interactions involved colors, movements, and sounds.

The skeletons of dinosaurs combined the strength required to support animals that weigh thousands or tens of thousands of kilograms with features that minimized the weight of the skeleton. Postcranial pneumatization was widespread in dinosaurs and pterosaurs; the open spaces in bone are believed to be the traces of air sacs like those in extant birds.

**Hips and legs**

Dinosaurs originated from small (about 1 m), agile terrestrial archosaurs. Some of these animals were bipedal and already had morphological changes in the hips that allowed the hindlimbs to be held beneath the body in an erect stance. In addition, the articulation of the ankle joint had been simplified so that it formed a straight-line hinge (mesotarsal joint; see Figure 19.3) rather than the complex articulation of several bones that characterized basal archosaurs. The novel ankle structure allowed the hindfeet to thrust backward forcefully without twisting. These two changes set the stage for the increase in body size that was so prominent in dinosaurs, but they required additional changes in the pelvis, and these changes distinguish the ornithischian and saurischian lineages of dinosaurs.

Early tetrapods had a sprawling posture, with the humerus and femur projecting more or less horizontally and a sharp bend at the elbow and knee. This posture is sufficient for small and medium-size tetrapods, but it does not work for large animals. Bones are far more resistant to force exerted parallel to their long axis (compressive force) than to force exerted at an angle to the long axis (shearing force). Thus, large extant mammals, such as rhinoceroses and elephants, support their weight on vertical limbs. Many dinosaurs were far larger than elephants, and the limbs of dinosaurs were also oriented vertically.
Changing the angle of the limbs solved the problem of weight-bearing but introduced a new problem. Among early tetrapods, muscles originating on the pubis and inserting on the femur protracted the leg (moved it forward), and muscles originating on the tail retracted the femur (moved it backward). The ancestral tetrapod pelvis, little changed from *Ichthyostega* through basal archosauriforms, was platelike (*Figure 19.13A*). The ilium articulated with one or two sacral vertebrae, and the pubis and ischium did not extend far anterior or posterior to the hip socket (acetabulum).

Because these animals had a sprawling posture, the femur projected horizontally and the pubofemoral muscles extended outward from the pelvis to insert on the femur. Thus, they were long enough to swing the femur through a large arc relative to the ground. But moving the legs under the body made those muscles shorter and less effective in moving the femur, because a muscle’s maximum contraction is about 30% of its resting length. The shorter muscles would have swung the vertical femur through a smaller arc and reduced the stride to a shuffle.

Dinosaurs solved that problem by moving the origins of the muscles to make them longer and combine upright stance with long strides. The saurischian (lizard-hipped) and ornithischian (bird-hipped) dinosaurs did that in different ways. In saurischians (*Figure 19.13B*), the pubis and ischium both became elongated and the pubis was rotated anteriorly, so that the pubofemoral muscles ran back from the pubis to the femur and were long enough to protract it. Ornithischians (*Figure 19.13C*) rotated the pubis posteriorly to lie against the ischium and pubofemoral muscles originated on the ilium. Derived ornithischians (*Figure 19.13D*) developed an anterior projection of the pubis (the prepubis) that extended beyond the anterior part of the ilium, providing an anterior origin for protractor muscles.

Although these changes were anatomically different, they were functionally the same—both produced hip articulations that allowed the legs to be held vertically beneath the pelvis to support heavy bodies with stride lengths that enabled dinosaurs to move rapidly and over long distances.

**Dinosaur lineages**

An estimated 1,500 to 2,500 species of dinosaurs roamed Earth during the Mesozoic, and a new species is named about every two weeks. Since the 1980s, Dinosauria has been considered to be a monophyletic lineage containing two monophyletic sister lineages, the bird-hipped dinosaurs (Ornithischia, Greek *ornis*, “bird”; *ischium*, “hip joint”) and the lizard-hipped dinosaurs (Saurischia) (*Figure 19.14*).

- All ornithischian dinosaurs were herbivores. They included hadrosaurs (duck-billed dinosaurs), stegosaurs, and ceratopsians (horned dinosaurs), among others. Ornithischians reached their greatest diversity in the Late Cretaceous.
- Saurischian dinosaurs include two lineages: Sauropoda (Greek *pous* “foot”) were long-necked, long-tailed
herbivores that reached their maximum diversity in the Late Jurassic; Theropoda (Greek ther, “wild beast”) were carnivores and reached their maximum diversity in the Late Cretaceous.

**19.8 Ornithischian Dinosaurs**

Body forms of ornithischians were diverse, and the elaborate crests, frills, and horns that decorated the heads of many species suggest that ornithischians had complex social behaviors. Many species probably lived in family groups or formed herds, and some species nested in colonies.

All ornithischians were herbivores, feeding on low-growing vegetation (mostly within 2 m of the ground). All had horny beaks, and all processed food orally—that is, they chewed. Chewing (reducing food to a pulp in the mouth before swallowing) is the norm for mammals, but outside of mammals, chewing is rare; most vertebrates either swallow prey whole or tear off and swallow chunks of their food.

Three major lineages of ornithischian dinosaurs are distinguished: the armored dinosaurs (Thyreophora), the horned dinosaurs (Marginocephalia), and the duck-billed dinosaurs (Ornithopoda).

**Thyreophora**

Thyreophorans (Greek thyreos, “shield”; phoros, “a bearer”) were the armored dinosaurs ([Figure 19.15](#)). Their name refers to the parallel rows of *osteoderms* (bones embedded in the skin) that extended from the neck to the tail, armor ing the back. The two major lineages, Stegosauria and Ankylosauria, were quadrupedal, although some basal forms were bipedal.
Stegosauria  Stegosaurs (Greek *stegos*, “roof”) were most abundant in the Late Jurassic, although some species persisted to the end of the Cretaceous. Stegosaurs were medium-size to large—up to 9 m—quadrupedal herbivores with small heads, short and sturdy forelegs, and long, columnar hindlegs. The short forelegs kept the head close to the ground, and stegosaurs may have browsed on ferns, cycads, and other low-growing plants. The skull was small for such a large animal and had a horned beak at the front of the jaws. The teeth were shaped like those of extant herbivorous lizards, and show none of the specializations seen in some other ornithischians, which appear to have been able to grind or cut plant material into small pieces that could be digested efficiently. Stegosaurs may have eaten large quantities of food without much chewing and used stone *gastroliths* (Greek *gastros*, “stomach”; *lithos*, “stone”) in a muscular gizzard to pulverize plant material.

The distinctive feature of stegosaurs was a double row of spines or leaf-shaped plates that extended along the vertebral column. In addition, all stegosaurs (except for *Stegosaurus*) had a long spine that projected upward and backward from the shoulder. These spines and plates were hypertrophied keels of the osteoderms that are characteristic of thyreophorans. In stegosaurs (*Stegosaurus, Kentrosaurus*) the keels of the osteoderms were elaborated into spikes or plates, whereas in *Ankylosaurus* (*Polacanthus, Euoplocephalus*) the osteoderms in some areas fused to each other, creating platelike armor. The silhouettes illustrate body forms but not relative sizes. (Data from Fastovsky and Weishampel 2016.)

The function of the plates of *Stegosaurus* has been a matter of contention for decades. Initially they were assumed to have provided protection from predators, and some reconstructions have shown the plates lying flat against the sides of the body as shields. A defensive function is not very convincing, however. Whether the plates were erect or flat, they left large areas on the sides of the body and the belly unprotected.

A role for the plates as heat exchangers initially seemed plausible. Grooves on the surface of the plates were interpreted as channels for blood vessels that could carry a large flow of blood to be warmed or cooled according to the needs of the animal. However, a reanalysis of the microstructure of the plates concluded that the channels merely carried nutrients to the overlying sheath that covered the plates, and would have had little, if any, role in thermoregulation.

The combinations of plates and spines were species-specific and dimorphic within a species. These characters suggest that the plates and spines identified species and sex during intraspecific behavioral interactions. The plates and spines increased the apparent size of a stegosaur when viewed from the side, and may have deterred both rivals and potential predators.

The tails of stegosaurs had large spines near their tips. These spines were almost certainly defensive structures, and a biomechanical analysis of the whipping motion of the tail of *Kentrosaurus* supports that interpretation. Using the tail muscle of an alligator as the basis for calculation, this study concluded that the tail tip of an adult *Kentrosaurus* could strike a predator at a velocity of 20–40 m/sec. At those speeds, the tip of a spine would have exerted enough force to penetrate skin and muscle to a depth of 30 cm or to pierce bony armor.

Ankylosauria  Ankylosaurs (Greek *ankyllos*, “stiffening”) were a group of heavily armored dinosaurs found in Jurassic and Cretaceous deposits in North America and Eurasia; the timing of their appearance may have been linked to the increase in size of carnivorous dinosaurs at that time. Ankylosaurs were quadrupedal ornithischians that ranged from 2 to 6 m long. They had short legs and broad bodies, with osteoderms that were fused on the neck, back, hips, and tail to produce large shieldlike pieces. Bony plates also covered the skull and jaws, and in *Euoplocephalus* even the eyelids had bony armor.
Ankylosaurs must have been difficult animals to attack. Some species of nodosaurids had spines projecting from the back and sides of the body, while derived species of ankylosaurids had a lump of bone at the end of the tail that could be swung like a club. Even species of ankylosaurs without clubs or spines had broad, flat bodies with armored backs and sides, and the act of merely lying flat on the ground might have been an effective defensive tactic.

**Marginocephalia**

Marginocephalians (Latin *margo*, “border”) take their name from the bony shelf at the rear of the skull. Two lineages of marginocephalians are distinguished: ceratopsians and pachycephalosaurs (Figure 19.16).

**Ceratopsia**  Ceratopsians (Greek *keras*, “horn”; *opsis*, “appearance”), the horned dinosaurs, were the most diverse marginocephalians. Ceratopsians appeared in the Late Jurassic or Early Cretaceous. The distinctive features of ceratopsians were the frill over the neck, which was formed by an enlargement of the parietal and squamosal bones; a parrotlike beak; and teeth that were arranged in batteries in each jaw, where they formed a series of knifelike edges rather than a solid surface. The feeding method of ceratopsians probably consisted of shearing vegetation into short lengths.

Although ceratopsians were quadrupedal, they were derived from a bipedal ancestor. Early ceratopsians, such as *Protoceratops*, were small (cat-size to sheep-size), had a simple frill, and lacked nasal horns (Figure 19.17A). About 90 Ma, a lineage of larger animals (rhinoceros-size to elephant-size) appeared sporting a more elaborate frill, long brow horns, and nasal horns. Two groups of these

![Figure 19.16 Simplified phylogeny of Marginocephalia.](image)

![Figure 19.17 Elaboration of the frill and horns of ceratopsians.](image)
derived ceratopsians can be distinguished. In short-frilled ceratopsians, such as *Triceratops*, the frill extended back over the neck, whereas in the long-frilled forms, such as *Titanoceratops*, the frill extended half the length of the trunk (Figure 19.17C,D).

**Pachycephalosauria**  Pachycephalosaurs were a group of small to medium-size (1–5 m) bipedal dinosaurs that lived during the Cretaceous. A distinctive feature of this lineage was a pronounced thickening of the skull roof (Greek *pachys*, “thick”) in some species, and an array of bony projections on the skull of other species (Figure 19.18).

**Ornithopoda**  Ornithopods lived from the Middle Jurassic to the end of the Cretaceous (Figure 19.19). Most species were medium-size, although the largest species rivaled sauropods in size. Small species were largely bipedal, and the largest species probably moved mostly on four legs.

**Hadrosauridae**  Hadrosaurs (Greek *hadros*, “bulky”) were the last group of ornithopods to evolve, appearing in the mid-Cretaceous, and they were also the most speciose lineage. These were large animals, some reaching lengths of more than 15 m and weights greater than 13,000 kg. The anterior portion of the jaws was toothless and sheathed in a horny beak, and a remarkable battery of teeth occupied the rear of the jaws. On each side of the upper and lower jaws were four tooth rows, each containing about 40 teeth packed closely side by side to form a massive tooth plate. Several sets of replacement teeth lay beneath those in use, so a hadrosaur had several thousand teeth in its mouth, of which several hundred were in use simultaneously—perhaps the most advanced vertebrate chewing apparatus ever. Fossilized stomach contents of hadrosaurs consist of pine needles and twigs, seeds, and fruits of terrestrial plants.

**Social behavior of ornithischian dinosaurs**  Although it is impossible to know what a dinosaur was doing in the last moments before it died and embarked on the long trail to becoming a fossil, multiple discoveries of fossil beds that contain many individuals of the same species of ornithischian dinosaur support the hypothesis that they formed
herds. In many cases, the material surrounding the fossils represents a sudden fatal event such as a lahar (volcanic mudflow) or deep deposits of volcanic ash, reinforcing the impression that the fossils represent a group of individuals that lived and died together.

**Ceratopsians** The frills and horns of ceratopsians (see Figure 19.17) were probably elements of social behavior, especially in male-male competition. Observations of modern horned mammals suggest that differences in the size of the frill and the length and arrangement of the horns were associated with different behaviors:

- **Species of antelopes with small horns engage in side-on displays with other males.** Competing males swing their heads sideways against the flank of their opponent in a comparison of strength. *Protoceratops* and other early ceratopsians may have used displays like this.

- **Deer and elk have large antlers, and males engage with each other head-on, interlocking their antlers and twisting their necks as each individual attempts to knock the other off its feet.** The sturdy horns of *Triceratops* and other short-frilled ceratopsians would have been suitable for trials of strength of this sort. Some fossils of *Triceratops* have wounds on the face and frill that match the size and spacing of the large brow horns.

- **Moose have enormous antlers that consist mostly of flat surfaces.** Rival males face each other head-on, twisting and shaking their heads to emphasize the breadth of their antlers. This comparison of antler size is often sufficient to determine dominance, and when moose do engage in trials of strength they are back-and-forth shoving contests. Long-frilled ceratopsians, such as *Chasmosaurus*, may have engaged in these sorts of displays.

The nasal and brow horns of ceratopsians would have been formidable weapons and were probably used for defense against carnivorous dinosaurs. A herd of ceratopsians might have used the same defense as some modern horned mammals, forming a defensive ring when a predator approached, with the adults on the outside, facing the predator, and the juveniles sheltered in the center of the ring.

**Pachycephalosaurs** Mature pachycephalosaur males are believed to have used their domed heads in male-male combat for territories or access to mates, with different configurations of the dome and its projections corresponding to different methods of combat (Figure 19.20).

**Hadrosaurs** The nasal regions of hadrosaurines were greatly enlarged, and may have been surrounded by soft tissue that could be inflated by exhaled air, rather like the nasal regions of male elephant seals. (Figure 19.21A–C). The heads of lambeosaurine hadrosaurs were crowned by hollow crests. These crests were sexually dimorphic—much larger in males than in females (Figure 19.21D,E). The crest of a male *Parasaurolophus* was a curved structure that extended back over the shoulders. Air in the hollow crest flowed from the external nares backward through the crest and then forward to the internal nares, which were located in the palate just anterior to the eyes (Figure 19.21F).

The inflatable proboscis of hadrosaurines and the hollow crests of lambeosaurines were probably used for visual displays and for vocalizations. Acoustic analysis of the ears of lambeosaurines indicates that they would have been able...
to hear the sound frequencies produced by the resonating columns of air in the nasal passages.

**Nesting and parental care by ornithischians**

Inferences about parental care by dinosaurs rest on a firmer basis than inferences about their social behavior. Not only do we have observations of parental care by the extant bracketing groups, crocodylians and birds, but thousands of nests of nonavian dinosaurs have been discovered.

Ornithischian dinosaurs laid eggs in an excavation that might have been filled with rotting vegetation to provide both heat and moisture for the eggs. Similar methods of egg incubation are used by crocodylians and by the brush turkeys of Australia.

Some ornithischians probably provided an extended period of parental care. For example, a nest of the hadrosaur *Maiasaura* (Greek *maia*, “good mother”) uncovered in the Late Cretaceous Two Medicine Formation in Montana contained 15 juveniles that were about 1 m long (approximately twice the size of hatchlings found in the same area), indicating that the group remained together after they hatched. The teeth of the baby hadrosaurs showed that they had been feeding; some teeth were worn down to one-fourth of their original length. It seems likely that a parent remained with the young.

Other fossils suggest that *Maiasaura* and another hadrosaur, *Hypacrosaurus*, grew to one-fourth of adult size before they left the nesting grounds, and that another ornithopod found at the same site grew to half its adult size. A nest of the ceratopsian *Protoceratops andrewsi* from a Late Cretaceous fossil deposit in Mongolia contained 15 juveniles that were larger than a hatchling from the same area, again suggesting that hatchlings remained at the nest and were cared for by a parent. Discovery of a single adult *Psittacosaurus* with 34 babies suggests that juveniles from several clutches may have assembled in a creche, a behavior that also occurs in several species of crocodylians.

**19.9 Herbivorous Saurischians**

Saurischians radiated into two very different lineages: the herbivorous sauropods and the carnivorous theropods. The sauropods included the gigantic long-necked, long-tailed dinosaurs that are the centerpieces of paleontology halls at many museums, but those are the derived forms. Although their ancestors were bipedal, derived sauropods were quadrupedal. Basal sauropodomorph dinosaurs (prosauropods), were most diverse in the Late Triassic and Early Jurassic. Prosauropods were not as large as their descendants; *Platynotus*, with a length of 6 m, was among the largest prosauropods.

**The structure of sauropods**

Prosauroptery had long necks and small heads; *Platynotus* had 10 cervical vertebrae, 15 trunk vertebrae, 3 sacral vertebrae (the vertebrae that connect the hips to the vertebral column), and about 46 caudal vertebrae. The long necks of prosauropods suggest that they were able to browse on plant material at heights up to several meters above the ground. The ability to reach tall plants might have been a significant advantage during the shift from the low-growing *Dicroidium* flora to the taller bennettitales (extinct...
frond-bearing plants allied to cycads) and conifers that occurred in the Late Triassic.

The derived sauropods of the Jurassic and Cretaceous—neosauropods—were enormous. Gigantism evolved independently in different lineages, which suggests that the ability to grow to a large body size is an ancestral character of the sauropodomorph lineage. Neosauropods were the largest terrestrial vertebrates that have ever existed. The largest of them may have exceeded 30 m in length and weighed 50,000 kg. (For comparison, a large African elephant is about 5 m long and weighs 4,000–6,000 kg.)

Long necks increased the area in which a sauropod could feed. The length of the necks of neosauropods resulted both from lengthening the cervical vertebrae and from increasing their number, which rose from 10 in prosauropods to a minimum of 12 and a maximum of 19 in neosauropods. The neck became shorter in neosauropods as the number of dorsal vertebrae decreased from 15 in prosauropods to as few as 9 in neosauropods. The connection between the vertebral column and the hips was increased to 5 sacral vertebrae in neosauropods, and their tails contained 80 or more caudal vertebrae.

Neosauropods had remarkably small heads in proportion to the size of their bodies, perhaps because a large head at the end of a long neck would exert too much leverage. One major group of neosauropods, macronarians ("big nostrils"), had short, deep snouts with enormous nasal openings near the top of the skull, and spatulate teeth, which extended the full length of the jaws. *Camarasaurus* had a maximum of three replacement teeth in position for each active tooth, and teeth were replaced every 62 days. The forelimbs of macronarians were longer than their hindlimbs, so their backs sloped downward.

The other major lineage of neosauropods, diplodocoids, had long, flat snouts. Current interpretations place the nasal openings near the front of the snout. Diplodocoids had peglike teeth that were limited to the front of the jaws. Each *Diplodocus* tooth had 5 replacement teeth in position, and its active teeth were replaced every 35 days. The forelimbs of diplodocoids were shorter than the hindlimbs and they had long tails with a whiplike tip (Figure 19.22).

Simple teeth were sufficient for neosauropods because they were bulk feeders, consuming enormous quantities of food and digesting it slowly. They used their teeth to strip twigs and leaves from trees, but they did little oral processing of that material. Instead, their large gastrointestinal tracts allowed slow rates of passage, giving symbiotic microorganisms time to ferment the food and releasing volatile fatty acids that were absorbed across the wall of the intestine.

Sauropods were enormously heavy, and the skeletons of large sauropods clearly reveal selective forces favoring a combination of strength with light weight. The axial skeleton, vertebrae, and ribs were strongly pneumatized (i.e., contained many air spaces known as pleurocoels). The pneumatization moved progressively backward in neosauropods, eventually including the hips and tail vertebrae. The arches of the vertebrae acted like flying buttresses on a large building, while the neural spines held a massive and possibly elastic ligament that helped support the head, neck, and tail (Figure 19.23). In cross section, the trunk was deep, like that of an elephant.

Fossil trackways of sauropods show that the legs were held under the body with the left and right feet only a single foot width apart. The limbs were held straight in an elephantlike pose and moved fore and aft parallel to the midline of the body. This morphology produces the straight-legged locomotion familiar in elephants, and sauropods probably walked with an elephantlike gait, holding their

Figure 19.22 Macronarian and diplodocoid sauropods differed in body proportions and skull shapes. (A) Macronarians had long forelegs, and their backs sloped downward from the shoulders. With extremely long necks, they may have browsed from treetops; some reconstructions even show them standing on their hindlegs to extend their reach. The skulls of macronarians were boxy, and spatulate teeth extended the length of the jaws. The external nares of macronarians (arrow) were high on the face and were as large as, or larger than, the eyes. (B) Diplodocoids had short forelegs, so their backs sloped down from the hips to the shoulders. Diplodocoid necks were long, although not as long as those of macronarians, and their heads were closer to the ground. They may have fed on low-growing vegetation, swinging the head in an arc to reach a large area. Diplodocoids had long, flat snouts; peglike teeth in the front of the jaws, and long tails with a whiplike tip. Current interpretations place the external nares near the front of the snout (arrow). (From Fastovsky and Weishampel 2005, illustrations by John Siddick.)
neck erect and their tails in the air. Sauropod trackways preserved in many parts of the world reveal the immense size of these animals (Figure 19.24).

Social behavior of sauropods

Sauropods lacked frills and other sexually dimorphic display structures of the sort seen among ornithischian dinosaurs, but that does not mean that social behavior was entirely absent. After all, extant crocodylians lack sexually dimorphic ornaments, yet they have an extensive repertoire of social behaviors. Still, the evidence for sociality by sauropods is so sparse that we can guess that sauropods had less extensive social interactions than ornithischians did.

An analysis of oxygen isotope ratios in the bones of *Camarasaurus* suggests that these sauropods made seasonal migrations of several hundred kilometers between upland and lowland environments. We cannot tell whether the dinosaurs traveled as individuals moving along the same route at the same time of year or as a cohesive group containing both adults and juveniles. Evidence of possible herd behavior by sauropods may be revealed by a series of tracks found in Early Cretaceous sediments at Davenport Ranch in Texas. These tracks show the passage of 23 sauropods in a group that appears to have moved in a structured fashion, with young animals in the center, surrounded by adults.

Another line of evidence comes from sites that preserve multiple individuals of a restricted age range of a single species of dinosaur. These associations suggest that juveniles lived in groups apart from adults, a phenomenon that has been observed in some extant species of grazing mammals. Several age-restricted sites of this sort have been discovered—for example, the Mother’s Day Quarry, a Late Jurassic site in Montana, contains numerous fossils of juveniles of a Diplodocus-like sauropod, and the Late Cretaceous Big Bend Alamosaurus site contains only juveniles of the sauropod *Alamosaurus sanjuanensis*.

Nesting and parental care by sauropods

Concentrations of nests and eggs ascribed to sauropods in an Early Jurassic site in South Africa and in Cretaceous deposits in southern France and Patagonia suggest that these animals had well-defined nesting grounds to which they returned year after year. Eggs thought to be those of the large sauropod *Hypselosaurus priscus* have been found in association with fossilized vegetation similar to that used by alligators to construct their nests. The orientation of the nests suggests that each female dinosaur probably deposited about 50 eggs. The eggs had an average volume of 1.9 L (about 40 times the volume of a chicken egg). Fifty of these eggs together would have weighed about 100 kg, or 1% of
the estimated body weight of the mother. Crocodylians and large turtles have egg outputs that vary from 1% to 10% of the adult body mass, so this estimate for Hypselosaurus seems reasonable.

Some nesting sites of sauropods have revealed astonishing quantities of eggs. During the Late Cretaceous, the Auca Mahuevo fossil site in Patagonia was a flood plain drained by shallow stream channels. Thousands of individuals of an unidentified species of large sauropod dinosaur journeyed here to construct nests, creating five layers of egg beds that extended for several kilometers and reached densities of 11 eggs per m². The eggs, which were roughly spherical, had diameters between 12 and 15 cm, with 20–40 eggs in each clutch. The eggs in a clutch were stacked on top of one another in two or three layers. There is no evidence of parental care. Indeed, considering the size of an adult sauropod and the dense spacing of the clutches, any loitering by an adult would have been more likely to crush eggs than protect them.

We do not yet have direct evidence of parental care by sauropods, but a nest of the prosauropod Massospondylus carinatus in South Africa may hint at parental care. The embryos in this nest appeared to be close to full term, but the ventral portions of the pelvic girdles were poorly developed, the heads were enormous in relation to the bodies, and teeth were virtually absent. This combination of characters would have made it difficult for the hatchlings to move about or feed themselves, and supports the inference that adults of this species of sauropod might have cared for their young.

19.10 Carnivorous Saurischians

In contrast to the herbivorous sauropods, the theropod lineage of saurischians was primarily carnivorous. Basal theropods were small, lightly built predators with long arms and legs. The hands contained three fingers and were held in the same position as human hands—palms inward. These theropods used their hands in a clapping motion to seize prey andhold it while they dismembered it with their jaws.

Derived theropod dinosaurs (coelurosaurs) included three general types of animals (Figure 19.25): predators that attacked large prey using their jaws as weapons (tyrannosauroids), fast-moving predators that seized small prey with their forelimbs (ornithomimosaurs), and fast-moving predators (maniraptorans). All theropods were fleet-footed; computer models suggest that ornithomimosaurs and maniraptors could reach speeds of 50–60 km/h, and even tyrannosaurs may have been able to sprint at 40 km/h.

**Tyrannosauroidea**

Early tyrannosauroids were small and lightly built with long arms and legs. Although derived tyrannosaurs were very large, the distinctive features of the lineage appeared in the early small species. The evolutionary history of tyrannosaurs proceeded in three stages starting in the Middle Jurassic. In the first stage, the skull was strengthened, the anterior upper teeth were serrated and the jaw muscles were powerful. The second stage, in the Early Cretaceous, produced a miniature tyrannosaur: *Raptorex kriegsteini* was only 3 m long (compared with 15 m for *Tyrannosaurus rex*), but it had nearly all the distinctive features of tyrannosaurs, including a large skull, tiny forelimbs, and long hindlimbs. In the third stage, which extended throughout the rest of the Cretaceous, tyrannosaurs increased in size.

The tiny forelegs of tyrannosauroids are puzzling. The arms were too short to reach the mouth, and the third finger had been lost, yet the arm bones were robust and the fingers were tipped with large claws. These characters suggest that the arms and hands were not vestigial; they had a function, but we don’t know what it was.

The teeth of large tyrannosauroids were as long as 15 cm, dagger shaped with serrated edges, and driven by powerful jaw muscles. Marks from the teeth of predatory dinosaurs are sometimes found on fossilized dinosaur bones, and these records of prehistoric predation provide a way to estimate the force of a dinosaur’s bite. The pelvis of a horned dinosaur (*Triceratops*) found in Montana bears dozens of bite marks from a *Tyrannosaurus rex*, some as deep as 11.5 mm. Fossilized feces (coprolites) deposited by a *Tyrannosaurus rex* in Saskatchewan, Canada, contained fragments of crushed bone from a juvenile ornithischian, indicating that tyrannosaurs could crush bone—a phenomenon unique to derived tyrannosaurs among diapsids. (Some mammals can crush bones, but no other diapsids are known to do so.) The distribution of teeth in the jaws of large tyrannosauroids allowed them to apply enormous bite forces (8,526–34,552 newtons) to localized areas to crack bones that were then pulverized by repeated bites.

Featherlike structures (filamentous protofeathers) appeared long before birds (the evolution of feathers is discussed in Chapter 21). New discoveries are pushing the origin of protofeathers back, and feathers may even be an ancestral character of Dinosauria. Not all dinosaurs had feathers, however; they are known from only a few ornithischians, and they are not universally present in saurischians. No featherlike structures have been identified in sauropods, but protofeathers and feathers are widespread among theropods, from coelurosaurs (the lineage that gave rise to birds; see Chapter 21) onward.

The occurrence of feathers among tyrannosauroids is perplexing. Filaments described as protofeathers in *Dilong* and *Yutyrannus*, two basal species of tyrannosauroids from the Early Cretaceous, but the skins of *Tyrannosaurus rex* and several other derived tyrannosauroids from the Late Cretaceous were covered by scales.

**Ornithomimisauria**

The ornithomimisaurians were lightly built, cursorial (specialized for running) coelurosaurs of the Cretaceous. Despite their name, which means “bird mimic,” the
ornithomimosaurs are not closely related to birds, but they had evolved into birdlike forms. *Ornithomimus* was ostrichlike in size, shape, and probably ecology as well. The legs were long with three weight-bearing toes, and the upper limb (femur) was more than twice as long as the lower limb (tibia), a ratio that is characteristic of cursorial tetrapods. *Ornithomimus* had a small skull on a long neck, and its toothless jaws were covered with a horny bill. The forelimbs were long, and three digits were retained on the hands. The inner digit was opposable and the wrist was flexible, making the hand an effective organ for capturing small prey. Like ostriches, *Ornithomimus* were probably omnivorous and fed on fruits, insects, small vertebrates, and eggs. Quite possibly they lived in groups, as do ostriches, and their long legs suggest that they inhabited open regions rather than forests.

**Maniraptora**

Maniraptors were active predators with long, slender legs and long arms with grasping fingers (their name means “predators that grasp with hands”). They were feathered—the body had a covering of downy feathers, and long pennaceous feathers on the arms, legs, and tail. Extremely long arms and hands; wings formed by vaned feathers; long claw on second digit of foot, backward-facing pubis. Like ostriches, *Ornithomimus* were probably omnivorous and fed on fruits, insects, small vertebrates, and eggs. Quite possibly they lived in groups, as do ostriches, and their long legs suggest that they inhabited open regions rather than forests.

**Figure 19.25** Simplified phylogeny of theropods. Bipedality, an ancestral character of theropods, was retained throughout the lineage. Feathers (protofeathers) may also have been ancestral, and some (but probably not all) species in the lineages shown here had feathers, at least on the arms, legs, or tail. Birdlike characters (reduction or complete loss of teeth and development of a beak) appeared independently in ornithomimids, oviraptosaurs, *Archaeopteryx*, and Aves (birds). The silhouettes illustrate body forms but not relative sizes. (Data from Fastovsky and Weishampel 2016.)
Derived maniraptorans (Paraves) had a huge claw on the second digit of the hind foot. Deinonychosaur means “terrible claw lizard,” and these maniraptorans deserved that name. Ranging in size from less than 1 m to at least 6 m, they were consummate predators, with large eyes and large brains. The claw on the second toe was sicklelike and was held off the ground during locomotion; only the third and fourth toes touched the ground. The arms and hands were long, with three long, claw-tipped fingers, one of which was a semiopposable thumb.

Although deinonychosaurs retained grasping hands, they used their feet to subdue prey. Focusing on the sickle-shaped claws, early interpretations proposed that Deinonychus used its claw to slash prey, perhaps hunting in packs and attacking large dinosaurs, disemboweling them with their talons. We are now confident that Deinonychus was feathered, and probably hunted individually, preying on animals smaller than itself (such as the small ornithopod Zephyrosaurus in this illustration). It probably pinned prey down with its claws, as modern falcons and hawks do, using its jaws to kill the prey and flapping its feathered arms for balance as the prey struggled. (A, Universal Images Group North America LLC/DeAgostini/Alamy Stock Photo; B, Emily Willoughby/CC BY-SA 3.0.)

**Social behavior of theropods**

Large terrestrial mammalian carnivores, such as tigers and large bears, are generally solitary. Adults of these species hunt individually, and groups form only when prey are concentrated in a small area—for example, Kodiak bears gather during the upstream migrations of salmon. Twelve large tyrannosaurs, *Albertosaurus sarcophagus*, found amid flood debris in the Late Cretaceous Horseshoe Canyon Formation in Alberta, Canada, might have been scavenging carcasses of animals killed in an earlier flood.

Some medium-size mammalian predators are more social; wolves, coyotes, and African hunting dogs live and hunt in family groups, for example, and smaller species of theropods, especially ornithomimids, might have been social. More than 20 juvenile *Sinornithomimus dongi* ranging from 1 to 7 years old were trapped in mud in a drying pond in western Mongolia, and 160 juvenile and adult individuals of *Avimimus* appear to have drowned while crossing a river in southern Mongolia. *Avimimus* was probably herbivorous, making it unlikely that these animals were drawn together by a temporary abundance of food.

**Nesting and parental care by theropods**

Recognition of parental care by theropods lagged behind discoveries of nests of ornithischian dinosaurs because of a mistaken identification in 1923. The fossil of a theropod dinosaur that apparently died while attending a nest of eggs was discovered in the Gobi Desert, but its significance was not recognized until 70 years later. The eggs, which were about 12 cm long and 6 cm in diameter, were thought to have been deposited by the small ceratopsian *Protoceratops andrewsi* because adults of that species were by far the most abundant dinosaurs at the site. The theropod was assumed to have been robbing the nest and was given the name *Oviraptor philoceratops*, which means “egg seizer, lover of ceratops.”

In 1993, paleontologists from the American Museum of Natural History, the Mongolian Academy of Sciences, and the Mongolian Museum of Natural History discovered a fossilized embryo in an egg identical to the supposed
Protoceratops eggs. To their surprise, the embryo was an Oviraptor nearly ready to hatch. With the benefit of hindsight, it is apparent that the adult dinosaur found in 1923 had been resting on its own nest, apparently trying to shelter its eggs from the sandstorm that buried the adult and the nest. Additional fossils of adult Troodon and Deinonychus, which like Oviraptor were maniraptorans, have subsequently been found sitting on eggs with their legs folded, arms extended, and bellies in contact with the eggs—the same posture that extant ground-nesting birds use when incubating eggs (Figure 19.27).

Male parental care appears to be ancestral for coelurosaurs, and is retained in the most primitive extant birds, paleognaths such as emus and ostriches. Thus, it is likely that male maniraptorans were the caregivers. Young maniraptorans may have remained with their male parent for extended periods, as do young emus and ostriches.

19.11 Gigantothermy and the Body Temperature of Dinosaurs

The popularization of “hot-blooded” dinosaurs in the 1970s initiated a controversy about body temperatures of dinosaurs and their mechanisms of thermoregulation that continued for several decades. The discovery that many dinosaurs had feathers has added a new dimension to the discussion, because insulation is one of the functions of feathers.

With a half-century of hindsight, it has become clear that the relationship between high metabolic rates and high body temperatures that is characteristic of extant vertebrates is not applicable to dinosaurs. Body temperatures and thermoregulatory mechanisms are closely related to body size, and most dinosaurs were much larger than any extant tetrapods. As a result, the link between high body temperatures and high metabolic rates seen among extant vertebrates does not apply to dinosaurs.

Gigantothermy is a form of thermoregulation characteristic of large animals that have low metabolic rates but nonetheless maintain body temperatures higher than their surroundings as a result of having low surface/volume ratios. Gigantotherms lose heat to the environment slowly. A biophysical model that assumes that dinosaurs had metabolic rates like those of extant crocodylians predicts that medium-size to large dinosaurs would have had body temperatures above 30°C with a day–night variation of less than 2°C even in far northern and southern latitudes. If hatching occurred in the spring, juveniles would have grown large enough to be gigantotherms before winter.

Thus, gigantothermy would have allowed large dinosaurs (both ornithischians and saurischians) to maintain stable core body temperatures with the low metabolic rates that are characteristic of extant turtles and crocodylians. Feathers would not have been necessary for thermoregulation; indeed, avoiding overheating would have been the major problem facing large dinosaurs. Skin imprints show that the bodies of large dinosaurs (tyrannosaurs, sauropods, and ornithopods) were scaly, not feathered. Repeated proposals that archosaurs had high metabolic rates ignore the physics of heat exchange and are incorrect.
Smaller dinosaurs (adult weights <100 kg) living at latitudes more than 45° north or south would not have had stable body temperatures without metabolic heat production, but heat production without insulation is ineffective. Thus, it is among these dinosaurs that we would expect to find feathers providing insulation. A dramatic reduction in body size occurred during the evolution of birds, from about 160 kg for basal maniraptorans to 100 g for the first birds. Fossils show that members of the Avialae (see Figure 19.25) were feathered, and they are assumed to have had high metabolic rates that maintained high and stable body temperatures, as will be discussed in Chapter 20.

### Summary

**Diapsids dominated the Mesozoic.**

All extant evolutionary lineages of vertebrates were present in the Mesozoic. Diapsida was the most abundant and diverse Mesozoic lineage.

Diapsids are characterized by a skull with two temporal fenestrae. The postorbital and squamosal bones form the base of the upper fenestra, and the jugal and quadratojugal bones form the lower arch.

Two lineages of diapsids are recognized. Extant lepidosauromorphs include the tuatara, lizards, and snakes, and archosauromorphs include the extant crocodylians and birds. Turtles (Testudines) are the sister group of Archosauria, which includes two major lineages: Pseudosuchia (now represented by crocodylians) and Ornithodira (birds, plus extinct pterosaurs and nonavian dinosaurs).

In the sea, lepidosauromorphs (ichthyosaurs, plesiosaurs, and others) diversified into adaptive zones occupied now by sharks, cetaceans, and other marine mammals. There were also Mesozoic diapsids (such as the long-necked plesiosaurs) that have no modern equivalents.

On land, archosaurians (crocodylomorphs, pterosaurs, and dinosaurs) filled the adaptive zones now occupied by mammals and birds. There were also forms (such as the enormous sauropod, theropod, and ornithopod dinosaurs) that have no present-day equivalents.

In addition to these now-extinct diapsids, the lineages that include extant lizards, snakes, turtles, and the tuatara began to diversify in the Mesozoic. Only mammals were poorly represented during the Mesozoic, although they were present and diversifying in terrestrial habitats.

**Lepidosauromorphs were a major component of the Mesozoic marine fauna.**

Lepidosaurus were not a prominent component of terrestrial faunas in the Mesozoic. Rynchocephalians were the most diverse terrestrial lepidosauromorphs during this time. Initially small terrestrial insectivores, they radiated into terrestrial and aquatic carnivores and terrestrial herbivores.

Ichthyosaurs evolved from lizardlike early forms to superbly streamlined aquatic predators with a body form that converged on that of fast-swimming cetaceans and sharks. Ichthyosaurs were viviparous, and the young were born tail-first, like those of extant cetaceans and sirenians.

Placodonts retained many characters of their terrestrial ancestors and were probably slow-swimming coastal herbivores, perhaps rather like extant sea cows.

Nothosaurs and pachypleurosaurs were elongated marine predators that probably pursued and captured fish.

Plesiosauroids radiated into two lineages: Pliosaurs had large heads and short necks and were probably pursuit predators. Plesiosaurs had small heads and long necks that could bend downward but not upward or laterally; plesiosaurs may have preyed on bottom-dwelling fishes and invertebrates.

Mosasaur were a lineage of varanid lizards that took to the sea, and early forms looked much like their terrestrial ancestors. Derived forms were streamlined and preyed on other marine diapsids.

**Crocodylomorphs also radiated in Mesozoic seas.**

Metriorhynchids were far more specialized for life in water than is any extant crocodylian; the limbs were modified as paddles, and the tail was hyparceral.

**Pterosaurs were the first flying vertebrates.**

Pterosaurs appeared in the Late Triassic, 80 million years before the earliest birds, and persisted until the end of the Cretaceous.

Pterosaurs radiated into all of the adaptive zones occupied by extant birds, and some that are not occupied by extant birds. Azhdarchids, which were probably terrestrial predators, may have been the most remarkable pterosaurs. Some azhdarchids could stand eye-to-eye with a giraffe, and the largest of them could have preyed on dinosaurs.

The primary wings of pterosaurs were formed by skin that was supported by the arm bones and an elongated fourth finger. Some pterosaurs had a posterior wing that extended between the pelvis and the hind legs. The skin of at least some pterosaurs was covered by fine, hairlike fuzz called pycnofibers.

All pterosaurs could fly, probably using a four-legged leap to get into the air. Tracks show that pterosaurs walked quadrupedally.

(Continued)
Pterosaurs were oviparous, and hatchlings were probably able to run and fly soon after leaving the nest. Birds and pterosaurs coexisted for about 100 Ma. The evolution of birds coincided with an increase in body size of pterosaurs, suggesting that birds may have outcompeted pterosaurs at small body sizes.

Two wholesale replacements of terrestrial vertebrate faunas occurred in the Triassic.

Herbivorous and carnivorous synapsids were the most abundant terrestrial vertebrates at the start of the Triassic. Basal pseudosuchians diversified into predators and herbivores in the Middle Triassic. Basal archosauriform and ornithodiran herbivores had largely replaced herbivorous synapsids by the end of the period.

Beginning in the Late Triassic, pseudosuchians and basal archosauriforms were replaced by dinosaurs. Herbivorous dinosaurs radiated in the Late Triassic, and carnivorous dinosaurs radiated in the Jurassic, after the end-Triassic extinction wiped out most pseudosuchian predators.

An increase in body size in dinosaurs required changes in the pelvis and associated musculature.

Large tetrapods hold their limbs vertically beneath the body because bone is more resistant to compressive force than to shearing force. As the limbs of dinosaurs moved to a vertical position, the origin of muscles that protract the femur shifted to maintain stride length. The anatomical changes in the pelvis characterize the two major lineages of dinosaurs.

- Saurischian dinosaurs had a long pubis that provided an anterior site for the origin of femoral protractors.
- Ornithischian dinosaurs rotated the pubis backward to lie parallel to the ischium and shifted the origin of femoral protractors to an anterior extension of the ilium or to an anterior projection of the pubis.

Ornithischian dinosaurs radiated into a wide variety of body forms.

The lineage included bipedal and quadruped species; all were herbivorous, had horny beaks, and chewed their food.

- Thyreophorans (armor-bearing dinosaurs, the stegosaurs and ankylosaurs) had rows of osteoderms on the back.
- Osteoderms were elaborated into leaf-shaped plates or spines in stegosaurs. Some ankylosaurs had spines, but they probably relied mostly on thick osteoderms for protection. Thyreophorans fed on low-growing vegetation.

Marginocephalians include the horned dinosaurs (ceratopsians) and the thick-headed pachycephalosaurs.

Although derived from a bipedal ancestor, derived ceratopsians were quadrupedal. Derived forms developed a frill that extended backward from the skull and horns that, like the horns and antlers of extant mammals, were probably used for defense and in social interactions with other individuals. Pachycephalosaurs remained bipedal; their distinctive feature was a thick skull roof that was probably advantageous during male-male combat.

Ornithopods appeared in the Middle Jurassic. Small species were largely bipedal, but the largest species were probably mostly quadrupedal.

Hadrosaurs (duck-billed dinosaurs) were the most speciose group of ornithopods. The largest species reached lengths of more than 15 m and weighed upward of 13,000 kg.

Hadrosaurs may have run bipedally to escape predators. They had dental batteries formed by thousands of teeth packed together to form tooth plates.

Many species of ornithischians probably formed herds. Social interactions probably included male-male competition for access to mates and territories. The plates and spines of stegosaurs, the frills and horns of ceratopsians, and the crests of lambeosaurines were probably visual and auditory signals in these interactions.

Hundreds of fossilized ornithischian nests have been discovered containing eggs, embryos, hatchlings, or older juveniles.

It appears that some ornithischians attended their nests, and hatchlings of some species probably remained with a parent for extended periods.

Saurichians radiated into two very different lineages.

Sauropods were quadrupedal herbivores, although they were derived from a bipedal lineage. Theropods were bipedal carnivores.

Sauropods had long necks, small heads, and long tails.

The earliest sauropods (prosauropods) were considerably smaller than derived sauropods (neosauropods). The two lineages of neosauropods, macronarians and diplodocoids, differed in the length of their necks and the structure of their skulls, teeth, and limbs. Neosauropods were the largest terrestrial animals that have ever existed.

Macronarians had boxy skulls with spatulate teeth running the full length of the jaws. Their forelegs were longer...
than their hindlegs. Macronarians probably browsed on high-growing vegetation, using their long necks for vertical reach.

Diplodocoids had long, flat snouts with peglike teeth at the front of the jaws. Their forelegs were shorter than their hindlegs, and they may have browsed on low-growing vegetation, using their long necks to cover a wide arc.

Some sauropods may have formed herds.
Fossilized tracks of sauropods indicate that they may have moved in herds with juveniles in the center, surrounded by adults. Other fossil sites preserve the remains of several subadult sauropods, all the same size, suggesting that juveniles of some species formed age-restricted herds, as do some extant mammals.

At least some sauropods had nesting grounds that were used by generation after generation.
Some species of sauropods may have constructed nests, but evidence for parental care of nests or hatchlings is weak.

Theropods included three general types of animals: tyrannosauroids, ornithomimids, and maniraptorans.
All theropods were carnivorous or omnivorous, and all were bipedal and fleet-footed. Many, but not all, were feathered, and the presence of feathers varied among species within some lineages.

Derived tyrannosaurs were enormous, heavily built predators.
Early tyrannosaurs were small and lightly built with long arms that they used to seize prey.
The forelimbs of derived tyrannosaurs were greatly reduced, and only two fingers remained. The arms were too short to lift food to the mouth, but they were robust and the fingers were clawed, suggesting that the arms and hands were not vestigial. Their function remains a mystery.

Derived tyrannosaurs had their weapons concentrated in their heads. Strong skulls, powerful jaw muscles, and serrated teeth allowed them to rip flesh from prey and crush bones.
Basal species of tyrannosaurs had filaments that are described as protofeathers, but fossilized skin impressions show that several derived tyrannosaurs were covered by scales.

Ornithomimids were ostrichlike in appearance and perhaps in their ecology.
Long hindlimbs with the femur longer than the tibia indicate that ornithomimids were cursorial. The forelimbs were long and had three grasping fingers that were used to seize prey.

Ornithomimids had long necks, small skulls, and toothless jaws. They were probably omnivorous and may have lived in groups, as ostriches do.

Maniraptorans were fast-moving predators with an enlarged talon on the second toe.
Maniraptorans retained the ancestral characters of long legs and long arms with grasping fingers. Feathers were extensively developed and included downy feathers covering the body and pennaceous feathers on the arms, legs, and tail of some species.
Oviraptosaurs were toothless and had horny jaws; they were probably herbivorous or omnivorous.

Deinonychosaur were pursuit predators. Current hypotheses propose that they were solitary predators that attacked animals smaller than themselves and used their talons to immobilize their prey while they tore at it with their teeth.

There is less evidence of social behavior by theropods than there is by saurischians.
Analogy with large mammalian carnivores suggests that large theropods were probably solitary. Some fossil deposits contain multiple individuals of the same species, raising the possibility that these represent mass-mortality events that overwhelmed a group of individuals.

At least some small species of theropods brooded their eggs in nests.
Fossils of maniraptorans show that adults brooded eggs as birds do, sitting on the clutch with their legs folded and their arms extended to cover the eggs. It is not known if parental care was present in tyrannosaurs.

The concepts of endothermy and ectothermy that describe thermoregulation of extant vertebrates cannot be transferred to dinosaurs.
Dinosaurs larger than about 100 kg would have been gigantotherms, meaning their low surface/volume ratios would have reduced the rate at which they lost heat to the environment. Computer models show that metabolic rates equivalent to those of extant crocodilians would have kept most medium-size to large dinosaurs warm; with higher metabolic rates, they would have overheated.

Only small dinosaurs would have required high metabolic rates and insulation. The transition from low to high metabolism in the avian lineage occurred during the extreme reduction in body size that characterized the evolution of birds.
Discussion Questions

1. Use the extant phylogenetic bracket method to test the hypothesis that male coelurosaur dinosaurs were the primary providers of care for eggs and young.

2. The necks of giraffes are the closest extant equivalent to the necks of sauropod dinosaurs. Two hypotheses have been proposed to explain the functional significance of the necks of giraffes, and those hypotheses can be applied to the necks of sauropods:
   a. Competing browsers hypothesis: The long neck makes more food resources available to a giraffe or sauropod by allowing it to reach up to browse on vegetation that is not available to short-necked browsers.
   b. Necks-for-sex hypothesis: Male giraffes and sauropods use their necks and heads to batter opposing males during intraspecific combat. Thus, long necks increase the fitness of males by increasing their opportunities to mate.

What predictions can you make about the relative lengths of the necks of male and female sauropods to test these hypotheses?

3. Extensive dinosaur faunas inhabited Arctic regions well beyond the polar circle. We know that northern regions were warmer during the Mesozoic than they are now; clearly they were warm enough for dinosaurs. But Arctic winters would have had long periods of dim light (twilight) in the Mesozoic, as they do now. How might dinosaurs have responded to the seasonal changes in day length in the Arctic?

4. Compare the use of inferences about the ecology, behavior, and physiology of extinct animals based on extant phylogenetic brackets with those based on analogies with extant forms—for example, the inferences in this chapter about the social behaviors of marginocephalian dinosaurs that were based on analogies with modern herbivorous mammals with horns or antlers. How might you test your conclusions in each case?

5. When a giraffe holds its neck in a vertical position, its brain is about 2 m above its heart. Contraction of the ventricle must create enough pressure to raise the blood to the level of the head and perfuse the brain (i.e., circulate blood through the brain). The arterial pressure at the aorta of a giraffe is approximately 200 mm Hg, twice that of a human. The brain of a sauropod dinosaur such as Barosaurus would have been about 9 m above the level of its heart, assuming it held its neck vertically. Calculate the aortic pressure required to perfuse the brain using the following information:
   a. The density of blood is 1.055 g/cm³ and the density of mercury 13.554 g/cm³.
   b. An aortic pressure of 10 mm Hg is needed to overcome resistance to blood flow in the carotid arteries leading from the heart to the brain.
   c. A blood pressure of 50 mm Hg at the head is required to perfuse the brain.

What inferences about the biology of sauropods can you draw from your calculation?

6. The concentration of oxygen in the atmosphere is currently ~21%, but it has been both higher and lower. At the start of the Permian it reached a maximum of 30–32%, then declined throughout the Permian and Triassic, reaching its minimum of 13–15% at the end of the Triassic. Dinosaurs and mammals both appeared in the Triassic, but dinosaurs flourished and radiated into a variety of large-bodied lineages, whereas mammals remained small and did not radiate into multiple lineages. Recall the characteristics of the respiratory systems of sauropsids and synapsids described in Chapter 14 to explain how the low concentration of atmospheric oxygen in the Permian may have favored the development of dinosaurs over mammals.

Additional Reading


