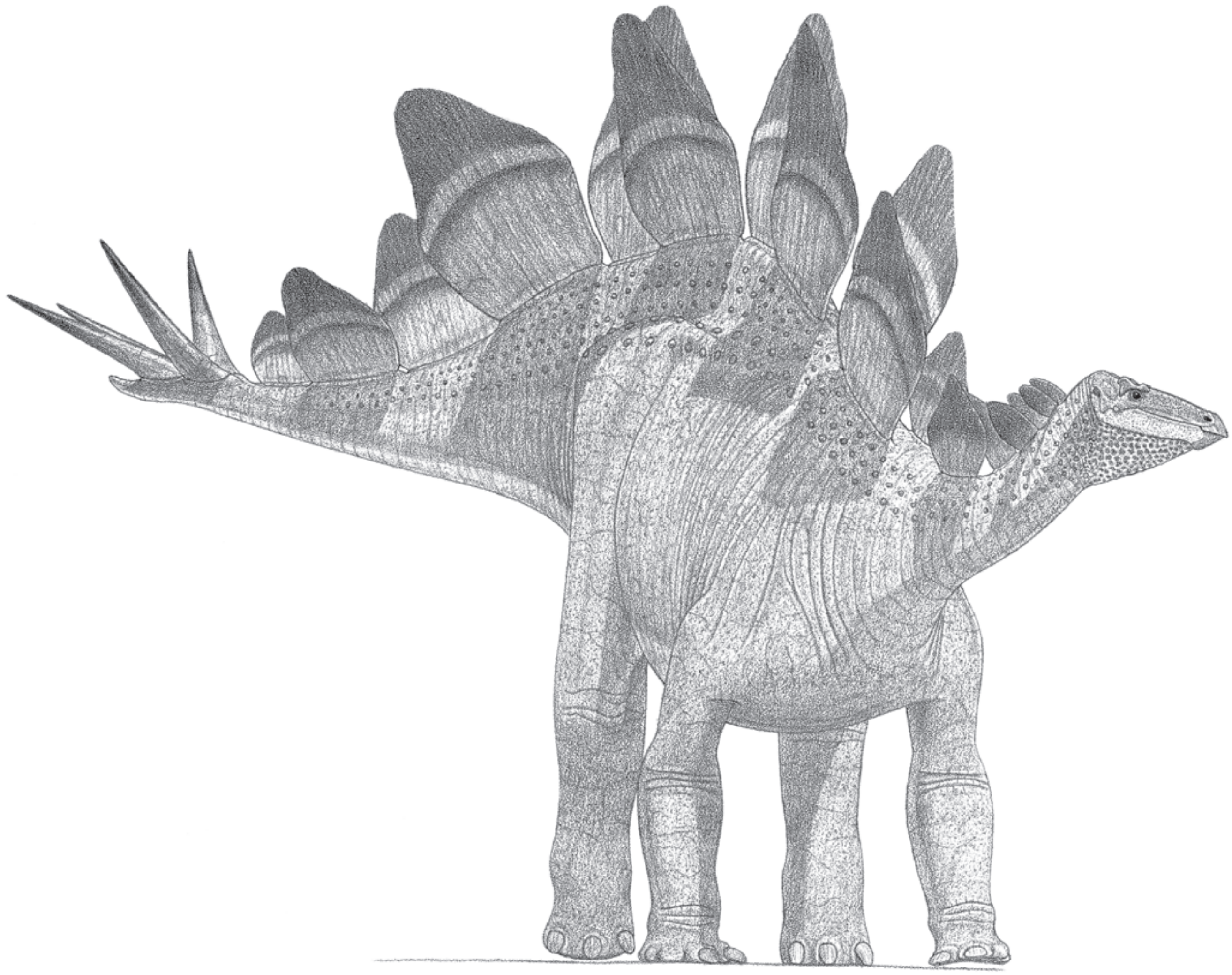
INTRODUCTION



The spectacular plated dinosaur *Stegosaurus*

HISTORY OF DISCOVERY AND RESEARCH

Dinosaur remains have been found by humans for millennia and probably helped form the basis for belief in mythical beasts including dragons. A few dinosaur bones were illustrated in old European publications without their true nature being realized. In the West the claim in the Genesis creation story that the planet and all life were formed just two thousand years before the pyramids were built hindered the scientific study of fossils. At the beginning of the 1800s the numerous three-toed trackways found in New England were attributed to big birds. By the early 1800s the growing geological evidence that Earth's history was much more complex and extended back into deep time began to free researchers to consider the possibility that long-extinct and exotic animals once walked the globe.

Modern dinosaur paleontology began in the 1820s in England. Teeth were found, and a few bones of the predatory *Megalosaurus* and herbivorous *Iguanodon* were published and named. For a few decades it was thought that the bones coming out of ancient sediments were the remains of oversized versions of modern reptiles. In 1842 Richard Owen recognized that many of the fossils were not standard reptiles, and he coined the term "Dinosauria" to accommodate them. Owen had pre-evolutionary concepts of the development of life, and he envisioned dinosaurs as elephantine versions of reptiles, so they were restored as heavy-limbed quadrupeds. This led to the first full-size dinosaur sculptures for the grounds of the Crystal Palace in the 1850s, which helped initiate the first wave of dinomania as they excited the public. A banquet was actually held within one of the uncompleted figures. These marvelous examples of early dinosaur art still exist.

The first complete dinosaur skeletons, uncovered in Europe shortly before the American Civil War, were those of small examples, the armored *Scelidosaurus* and the birdlike *Compsognathus*. The modest size of these fossils limited the excitement they generated among the public. Found shortly afterward in the same Late Jurassic Solnhofen sediments as the latter was the "first bird," *Archaeopteryx*, complete with teeth and feathers. The remarkable mixture of avian and reptilian features preserved in this little dinobird did generate widespread interest, all the more so because the publication of Charles Darwin's theory of evolution at about the same time allowed researchers to put these dinosaurs in a more proper scientific context. The enthusiastic advocate of biological evolution Thomas Huxley argued that the close similarities between *Compsognathus* and *Archaeopteryx* indicated a close link between the two groups. In the late 1870s Belgian coal miners came across the complete skeletons of iguanodonts that confirmed that they were three-toed semibipeds, not full quadrupeds.

At this time, the action was shifting to the United States. Before the Civil War, incomplete remains had been found on the Eastern Seaboard. But matters really got moving when it was realized that the forest-free tracts of the West offered hunting grounds that were the best yet for the fossils of extinct titans. This quickly led to the "bone wars" of the 1870s and 1880s in which Edward Cope and Charles Marsh, having taken a dislike for one another that was as petty as it was intense, engaged in a bitter and productive competition for dinosaur fossils that would produce an array of complete skeletons. For the first time it became possible to appreciate the form of classic Late Jurassic Morrison dinosaurs such as agile predatory *Allosaurus* and *Ceratosaurus*, along with *Apatosaurus*, *Brontosaurus*, *Diplodocus*, and *Camarasaurus*—which were really elephantine quadrupeds—the protoiguanodont *Camptosaurus*, and the bizarre plated *Stegosaurus*. Popular interest in the marvelous beasts was further boosted.

By the turn of the century, discoveries shifted to younger deposits such as the Lance and Hell Creek, which produced classic dinosaurs from the end of the dinosaur era including duck-billed *Edmontosaurus*, armored *Ankylosaurus*, horned *Triceratops*, and the great *Tyrannosaurus*. As paleontologists moved north into Canada in the early decades of the twentieth century, they uncovered a rich collection of slightly older Late Cretaceous dinosaurs including *Albertosaurus*, horned *Centrosaurus*, spiked *Styracosaurus*, and the crested duckbills *Corythosaurus* and *Lambeosaurus*.

Inspired in part by the American discoveries, paleontologists in other parts of the world looked for new dinosaurs. Back in Europe abundant skeletons of German *Plateosaurus* opened a window into the evolution of early dinosaurs in the Late Triassic. In southeastern Africa the colonial Germans uncovered at exotic Tendaguru the supersauropod *Giraffatitan* (was *Brachiosaurus*) and spiny *Kentrosaurus*. In the 1920s Henry Osborn at the American Museum in New York dispatched Roy Andrews to Mongolia in a misguided search for early humans that fortuitously led to the recovery of small Late Cretaceous dinosaurs, parrot-beaked *Protoceratops*, the "egg-stealing" *Oviraptor*, and the advanced, near-bird theropod *Velociraptor*. Dinosaur eggs and entire nests were found, only to be errantly assigned to *Protoceratops* rather than the oviraptorid that had actually laid and incubated them. As it happened, the Mongolian expeditions were somewhat misdirected. Had paleontologists also headed northeast of Beijing, they might have made even more fantastic discoveries that would have dramatically altered our view and understanding of dinosaurs, birds, and their evolution, but that event would have to wait another three-quarters of a century.

The mistake of the American Museum expeditions in heading northeast contributed to a set of problems that seriously damaged dinosaur paleontology as a science between the twentieth-century world wars. Dinosaurology became rather ossified, with the extinct beasts widely portrayed as sluggish, dim-witted evolutionary dead ends doomed to extinction, an example of the "racial senescence" theory that was widely held among researchers who preferred a progressive concept of evolution at odds with more random Darwinian natural selection. It did not help matters when artist/paleontologist Gerhard Heilmann published a seminal work that concluded that birds were not close relatives of dinosaurs, in part because he thought dinosaurs lacked a wishbone furcula that had just been found, but misidentified, in *Oviraptor*. The advent of the Depression, followed by the trauma of World War II—which led to the loss of some important specimens on the continent as a result of Allied and Axis bombing—brought major dinosaur research to a near halt.

Even so, public interest in dinosaurs remained high. The paleoart of Charles Knight made him famous. The *Star Wars–Jurassic Park* of its time, RKO's *King Kong* of 1933 amazed audiences with its dinosaurs seemingly brought to life. Two major film comedies, 1938's *Bringing Up Baby*, starring Cary Grant and Katherine Hepburn, and 1949's *On the Town*, featuring Gene Kelly and Frank Sinatra, involved climactic scenes in which sauropod skeletons at a semifictional New York museum collapsed because of the hijinks of the lead characters. Unfortunately, the very popularity of dinosaurs gave them a circus air that convinced many scientists that they were beneath their scientific dignity and attention.

Despite the problems, discoveries continued. In an achievement remarkable for a nation ravaged by the Great Patriotic War and suffering under the oppression of Stalinism, the Soviets mounted postwar expeditions to Mongolia that uncovered the Asian version of *Tyrannosaurus* and the enigmatic arms of enormous clawed *Therizinosaurus.* Equally outstanding was how the Poles took the place of the Soviets in the 1960s, discovering in the process the famed complete skeleton of *Velociraptor* engaged in combat with *Protoceratops*. They too found another set of mysterious long arms with oversized claws, *Deinocheirus*.

In the United States, Roland Bird studied the trackways of herds of Texas-sized Cretaceous sauropods before World War II. Shortly after the global conflict, the Triassic Ghost Ranch quarry in the Southwest, packed with complete skeletons of little *Coelophysis*, provided the first solid knowledge of the beginnings of predatory dinosaurs. Also found shortly afterward in the Southwest was the closely related but much larger crested theropod *Dilophosaurus* of the Early Jurassic.

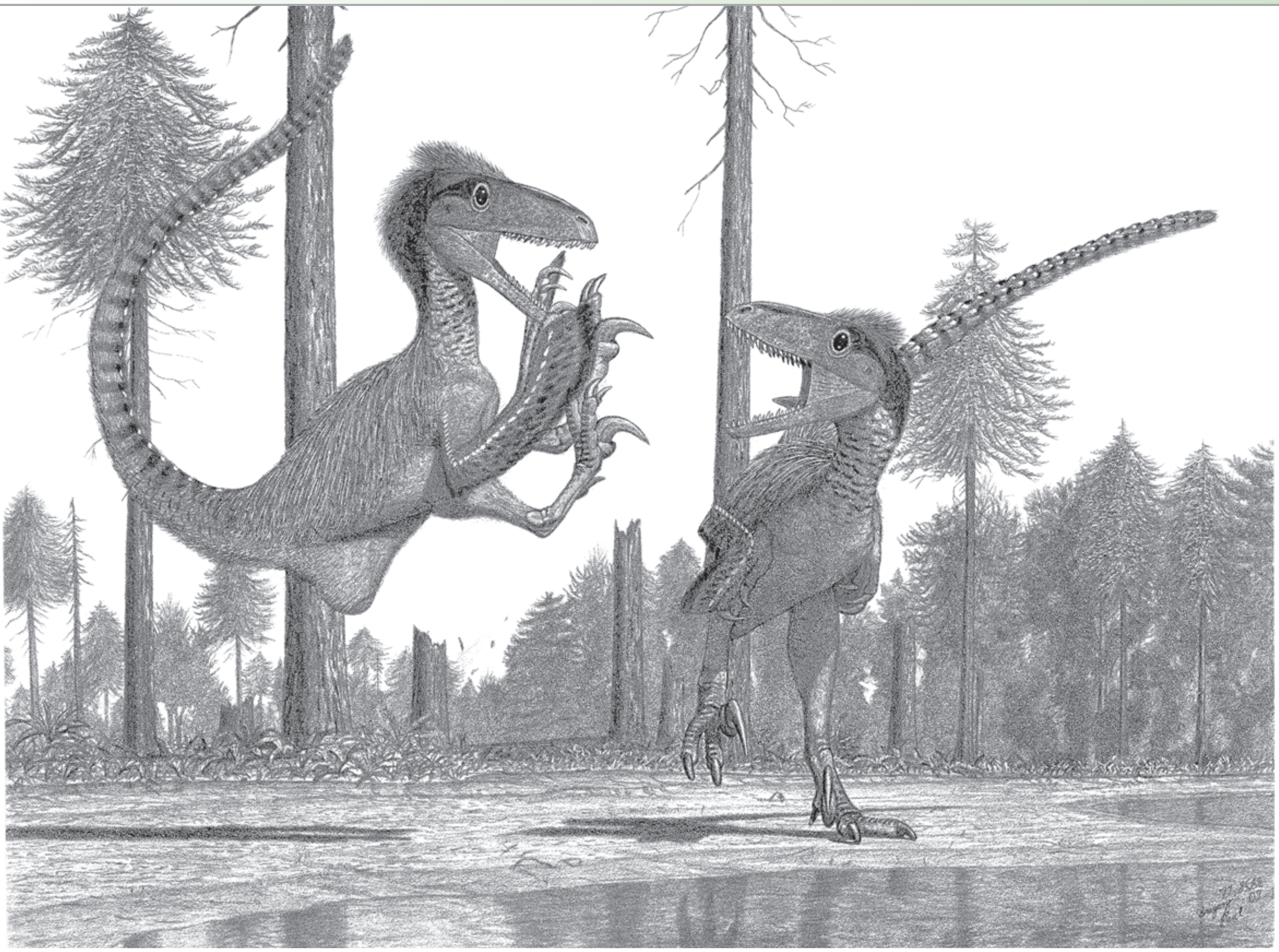
What really spurred the science of dinosaur research were the Yale expeditions to Montana in the early 1960s that dug into the little-investigated Early Cretaceous Cloverly Formation. The discovery of the *Velociraptor* relative *Deinonychus* finally made it clear that some dinosaurs were sophisticated, energetic, agile dinobirds, a point reinforced by the realization that it and the other sickle claws, the troodontids, as well as the ostrichlike ornithomimids, had fairly large, complex brains. These developments led John Ostrom to note and detail the similarities between his *Deinonychus* and *Archaeopteryx* and to conclude that birds are the descendants of energetic small theropod dinosaurs.

Realizing that the consensus dating back to their original discovery that dinosaurs were an expression of the reptilian pattern was flawed, Robert Bakker in the 1960s and 1970s issued a series of papers contending that dinosaurs and their feathered descendants constituted a distinct group of archosaurs whose biology and energetics were more avian than reptilian. Eventually, in the article "Dinosaur Renaissance" in a 1975 *Scientific American*, Bakker proposed that some small dinosaurs themselves were feathered. In the late 1970s, Montana native John Horner found baby hadrosaurs and their nests, providing the first look at how some dinosaurs reproduced. At the same time, researchers from outside paleontology stepped into the field and built up the evidence that the impact of an asteroid over six miles in diameter was the long-sought great dinosaur killer. This extremely controversial and contentious idea turned into the modern paradigm on the finding of a state-sized meteorite crater in southeastern Mexico dating to the end of the dinosaur era.

These radical and controversial concepts greatly boosted popular attention on dinosaurs, culminating in the *Jurassic Park* novels and films that sent dinomania to unprecedented heights. The elevated public awareness was combined with digital technology in the form of touring exhibits of robotic dinosaurs. This time the interest of paleontologists was elevated as well, inspiring the second and ongoing golden age of dinosaur discovery and research, which is surpassing that which has gone before. Assisting the work are improved scientific techniques in the area of evolution and phylogenetics, including cladistic genealogical analysis, which has improved the investigation of dinosaur relationships. A new generation of artists has portrayed dinosaurs with a "new look" that lifts tails in the air and gets feet off the ground to represent the more dynamic gaits that are in line with the more active lifestyles the researchers now favor. I noticed that the sickle-clawed dromaeosaurs and troodonts, as well as the oviraptorosaurs, possessed anatomical features otherwise found in flightless birds and suggested that these dinosaurs were also secondarily flightless.

Dinosaurs are being found and named at an unprecedented rate as dinosaur science goes global, with efforts under way on all continents. In the 1970s the annual Society of Vertebrate Paleontology meeting might have seen a half-dozen presentations on dinosaurs; now it is in the area of a couple of hundred. Especially important has been the development of local expertise made possible by the rising economies of many second-world nations, reducing the need to import Western expertise.

In South America, Argentine and American paleontologists collaborated in the 1960s and 1970s to reveal the first Middle and Late Triassic protodinosaurs, finally showing that the very beginnings of dinosaurs started among surprisingly small archosaurs. Since then, Argentina has been the source of endless remains from the Triassic to the end of the Cretaceous that include the early theropods *Eoraptor* and *Herrerasaurus*, supertitanosaur sauropods such as *Argentinosaurus*, *Futalongnkosaurus*, and *Dreadnoughtus*, and the oversized theropods such as



The dinobird *Deinonychus*

Giganotosaurus that preyed on them. Among the most extraordinary finds have been sauropod nesting grounds that allow us to see how the greatest land animals of Earth's history reproduced themselves.

In southern Africa excellent remains of an Early Jurassic species of *Coelophysis* verified how uniform the dinosaur fauna was when all continents were gathered into Pangaea. Northern Africa has been the major center of activity as a host of sauropods and theropods have filled in major gaps in dinosaur history. Australia is geologically the most stable of continents, with relatively little in the way of tectonically driven erosion to either bury fossils or later expose them, so dinosaur finds have been comparatively scarce despite the aridity of the continent. The most important discoveries have been of Cretaceous dinosaurs that lived close to the South Pole, showing the climatic extremes dinosaurs were able to adapt to. Glacier-covered Antarctica is even less suitable prospecting territory, but even it has produced the Early Jurassic crested avepod *Cryolophosaurus* as well as other dinosaur bones.

At the opposite end of the planet, the uncovering of a rich Late Cretaceous fauna on the Alaskan North Slope confirms the ability of dinosaurs to dwell in latitudes cold and dark enough in the winter that lizards and crocodilians are not found in the same deposits. Farther south, a cadre of researchers have continued to plumb the great dinosaur deposits of western North America as they build the most detailed sample of dinosaur evolution from the Triassic until their final loss. We now know that armored ankylosaurs were roaming along with plated stegosaurs in the Morrison Formation, a collection of sauropods has been exposed from the Early Cretaceous, and one new ceratopsian and hadrosaur after another is coming to light in the classic Late Cretaceous beds.

Now Mongolia and especially China have become the great frontier in dinosaur paleontology. Even during the chaos of the Cultural Revolution, Chinese paleontologists made major discoveries, including the first spectacularly long-necked mamenchisaur sauropods. As China modernized and Mongolia gained independence, Canadian and American researchers have worked with their increasingly skilled resident scientists, who have become a leading force in dinosaur research. It was finally realized that the oviraptors found associated with nests at the Flaming Cliffs were not eating the eggs but brooding them in a pre-avian manner. Almost all of China is productive when it comes to dinosaurs, and after many decades paleontologists started paying attention to the extraordinary fossils being dug up by local farmers from Early Cretaceous lake beds in the northeast of the nation.

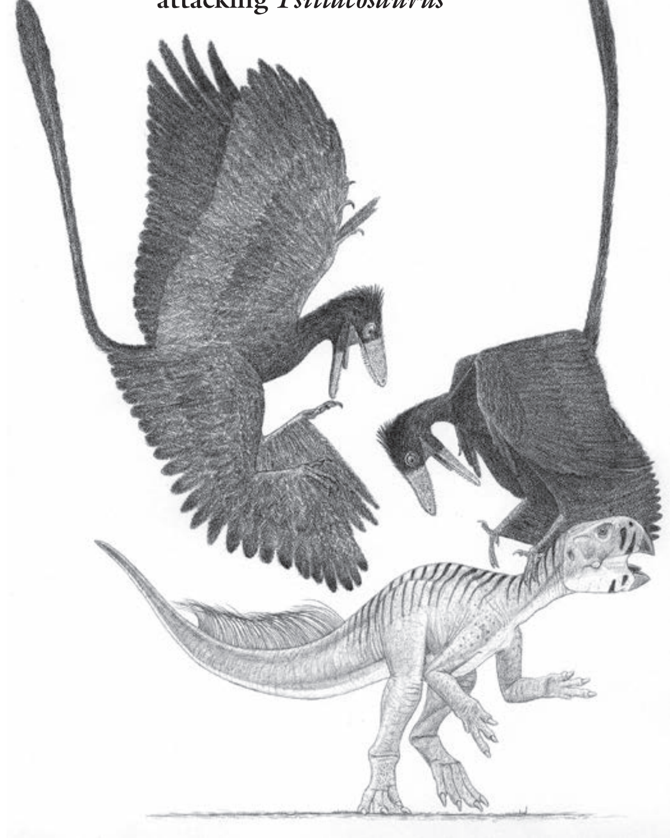
In the mid-1990s, complete specimens of small compsognathid theropods labeled *Sinosauropteryx* began to show up with their bodies covered with dense coats of bristly protofeathers. More recently it has been argued that it is often possible to determine the color of the feathers! This was just the start: the Yixian beds are so extensive and productive that they have become an inexhaustible source of beautifully preserved material as well as of strife, as the locals contend with the authorities for the privilege of excavating the fossils for profit—sometimes altering the remains to "improve" them—rather than for rigorous science. The feathered dinosaurs soon included the potential oviraptorosaur *Caudipteryx*. Even more astonishing have been the Yixian dromaeosaurs. These small sickle claws bear fully developed wings not only on their arms but on their similarly long legs as well. This indicates not only that dromaeosaurs first evolved as fliers but that they were adapted to fly in a manner quite different from the avian norm. The therizinosaur *Beipiaosaurus* looks like a refugee from a Warner Brothers cartoon. But the Yixian is not just about confirming that birds are dinosaurs and that some dinosaurs were feathered. One of the most common dinosaurs of the Early Cretaceous is the parrot-beaked *Psittacosaurus*. Although it was known from numerous skeletons across Asia found over the last eighty years, no one had a clue that its tail sported large, arcing, bristly spines until a complete individual with preserved skin was found in the Yixian. To top things off, the Yixian has produced the small ornithischian *Tianyulong*, which suggests that insulating fibers were widespread among small dinosaurs. There are new museums in China packed with enormous numbers of undescribed dinosaur skeletons on display and in storage.

On a global scale, the number of dinosaur trackways that have been discovered is in the many millions. This is logical in that a given dinosaur could potentially contribute only one skeleton to the fossil record but could make innumerable footprints. In a number of locations, trackways are so abundant that they form what have been called "dinosaur freeways." Many of the trackways were formed in a manner that suggests their makers were moving in herds, flocks, packs, and pods. A few may record the attacks of predatory theropods on herbivorous dinosaurs.

The history of dinosaur research is not just one of new ideas and new locations; it is also one of new techniques and technologies. The turn of the twenty-first century has seen paleontology go high tech with the use of computers for processing data and high-resolution CT scanners to peer inside fossils without damaging them. Dinosaurology has also gone microscopic and molecular in order to assess the lives of dinosaurs at a more intimate level, telling us how fast they grew, how long they lived, and at what age they started to reproduce. Bone isotopes are being used to help determine dinosaur diets and to state that some dinosaurs were semiaquatic. And it turns out that feather pigments can be preserved well enough to restore original colors. Meanwhile the *Jurassic World* franchise helps sustain popular interest in the group even as it presents an obsolete, prefeather image of the birds' closest relations.

The evolution of human understanding of dinosaurs has undergone a series of dramatic transformations since they were scientifically discovered almost two hundred years ago. This is true because dinosaurs are a group of "exotic" animals whose biology was not obvious from the start, unlike fossil mammals or lizards. It has taken time to build up the knowledge base needed to resolve their true form and nature. The latest revolution is still young. When I was a youth, I learned that dinosaurs were, in general, sluggish, cold-blooded, tail-dragging, slow-growing, dim-witted reptiles that did not care for their young. The idea that some were feathered and that birds are living descendants was beyond imagining. Dinosaur paleontology has matured in that it is unlikely that a reorganization of similar scale will occur in the future, but we now know enough

The flying dinosaur *Sinornithosaurus* attacking *Psittacosaurus*



about the inhabitants of the Mesozoic to have the basics well established. Sauropods will not return to a hippo-like lifestyle, and dinosaurs' tails will not be chronically plowing through Mesozoic muds. Dinosaurs are no longer so mysterious. Even so, the research is nowhere near its end. To date, over seven hundred valid dinosaur species in about five hundred genera have been discovered and named. This probably represents at most a quarter, and perhaps a much smaller fraction, of the species that have been preserved in sediments that can be accessed. And, as astonishingly strange as many of the dinosaurs uncovered so far have been, there are equally odd species waiting to be unearthed. Reams of work based on as-yet-undeveloped technologies and techniques will be required to provide further details about both dinosaur biology and the world in which they lived. And although a radical new view is improbable, there will be many surprises.

WHAT IS A DINOSAUR?

To understand what a dinosaur is, we must first start higher in the scheme of animal classification. The Tetrapoda are the vertebrates adapted for life on land—amphibians, reptiles, mammals, birds, and the like. Amniota comprises those tetrapod groups that reproduce by laying hard-shelled eggs, with the proviso that some have switched to live birth. Among amniotes are two great groups. One is the Synapsida, which includes the archaic pelycosaurs, the more advanced therapsids, and mammals, which are the only surviving synapsids. The other is the Diapsida. Surviving diapsids include the lizard-like tuataras, true lizards and snakes, crocodilians, and birds. The Archosauria is the largest and most successful group of diapsids and includes crocodilians and dinosaurs. Birds are literally flying dinosaurs.

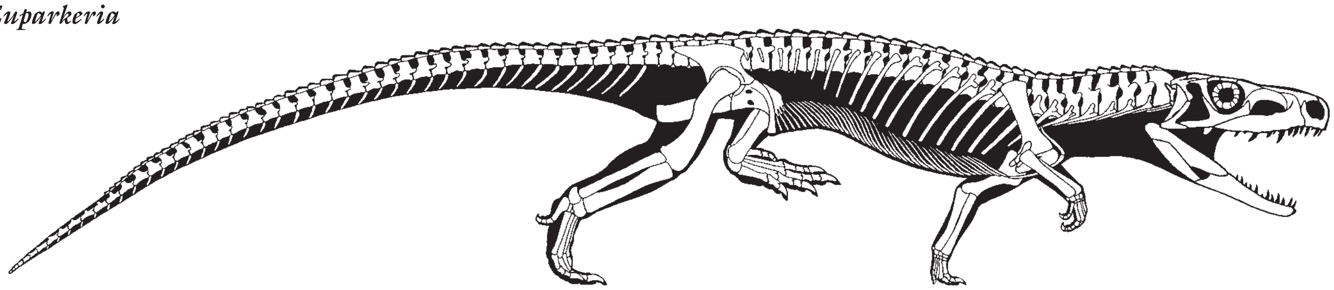
Archosaurs also include the basal forms informally known as thecodonts because of their socketed teeth, themselves a diverse group of terrestrial and aquatic forms that include the ancestors of crocodilians and the flying pterosaurs, which are not intimate relatives of dinosaurs and birds.

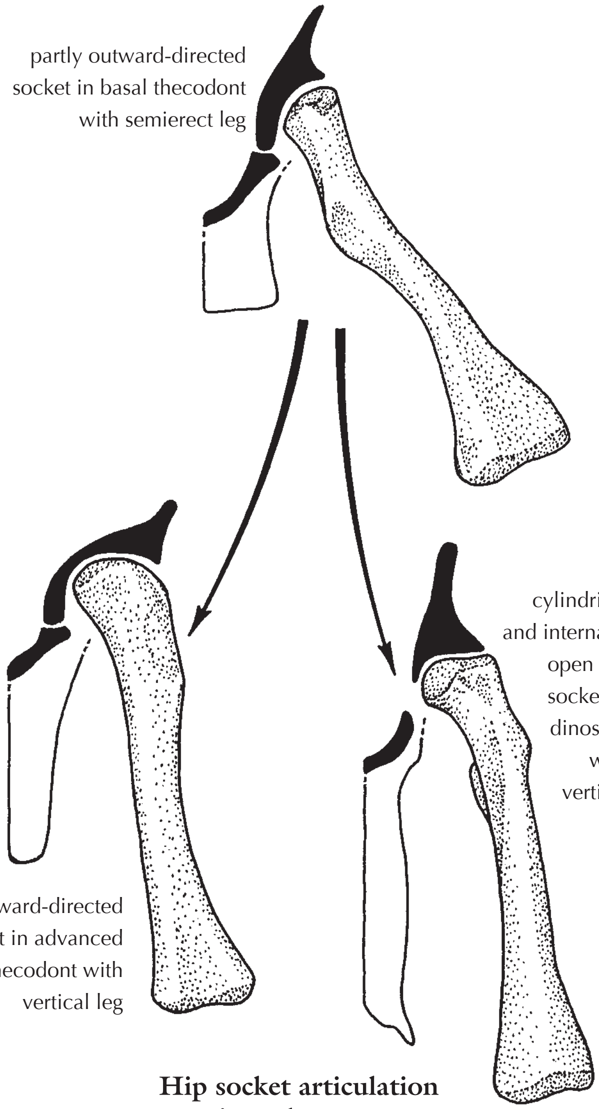
The great majority of researchers now agree that the dinosaurs were monophyletic in that they shared a common ancestor that made them distinct from all other archosaurs, much as all mammals share a single common ancestor that renders them distinct from all other synapsids. This consensus is fairly recent—before the 1970s it was widely thought that dinosaurs came in two distinct types that had evolved separately from thecodont stock, the Saurischia and Ornithischia. It was also thought that birds had evolved as yet another group independently from thecodonts. The Saurischia and Ornithischia still exist, but they are now the two major parts of the Dinosauria, much as living Mammalia is divided mainly into marsupials and placentals. Dinosauria is formally defined as the phylogenetic clade that includes the common ancestor of *Triceratops* and birds and all their descendants. Because different attempts to determine the exact relationships of the earliest dinosaurs produce somewhat different results, there is some disagreement about whether the most primitive, four-toed theropods were dinosaurs or lay just outside the group. This book includes them, as do most researchers.

In anatomical terms, one of the features that most distinguish dinosaurs centers on the hip socket. The head of the femur is a cylinder turned in at a right angle to the shaft of the femur that fits into a cylindrical, internally open hip socket. This allows the legs to operate in the nearly vertical plane characteristic of the group, with the feet directly beneath the body. You can see this system the next time you have chicken thighs. The ankle is a simple fore-and-aft hinge joint that also favors a vertical leg posture. Dinosaurs were "hind-limb dominant" in that they were either bipedal or, even when they were quadrupedal, most of the animal's weight was borne on the legs, which were always built more strongly than the arms. The hands and feet were generally digitigrade, with the wrist and ankle held clear of the ground. All dinosaurs shared a trait also widespread among archosaurs in general, the presence of large and often remarkably complex sinuses and nasal passages.

Aside from the above basic features, dinosaurs, even when we exclude birds, were an extremely diverse group of animals, rivaling mammals in this regard. Dinosaurs ranged in form from nearly bird-like types such as the sickle-clawed dromaeosaurs to

A basal archosaur,
Euparkeria





Hip socket articulation in archosaurs

rhino-like horned ceratopsians to armor-plated stegosaurs to elephant- and giraffe-like sauropods and dome-headed pachycephalosaurs. They even took to the skies in the form of birds. However, dinosaurs were limited in that they were persistently terrestrial. Although some dinosaurs may have spent some time feeding in the water like moose or fishing cats, at most a few became strongly amphibious in the manner of hippos, much less marine like seals and whales. The only strongly aquatic dinosaurs are some birds. The occasional statement that there were marine dinosaurs is therefore incorrect—these creatures of Mesozoic seas were various forms of reptiles that had evolved over the eons.

Because birds are dinosaurs in the same way that bats are mammals, the dinosaurs aside from birds are sometimes referred to as "nonavian dinosaurs." This usage can become awkward, and in general in this book dinosaurs that are not birds are, with some exceptions, referred to simply as dinosaurs.

Dinosaurs seem strange, but that is just because we are mammals biased toward assuming the modern fauna is familiar and normal, and past forms are exotic and alien. Consider that elephants are bizarre creatures with their combination of big brains, massive limbs, oversized ears, a pair of teeth turned into tusks, and noses elongated into hose-like trunks. Nor were dinosaurs part of an evolutionary progression that was necessary to set the stage for mammals culminating in humans. What dinosaurs do show is a parallel world, one in which mammals were permanently subsidiary and the dinosaurs show what largely diurnal land animals that evolved straight from similarly day-loving ancestors should actually look like. Modern mammals are much more peculiar, having evolved from nocturnal beasts that came into their own only after the entire elimination of nonavian dinosaurs. While dinosaurs dominated the land, small nocturnal mammals were just as abundant and diverse as they are in our modern world. If not for the accident of the later event, dinosaurs would probably still be the global norm.

DATING DINOSAURS

How can we know that dinosaurs lived in the Mesozoic, first appearing in the Late Triassic over 230 million years ago and then disappearing at the end of the Cretaceous 66 million years ago?

As gravels, sands, and silts are deposited by water and sometimes wind, they build up in sequence atop the previous layer, so the higher in a column of deposits a dinosaur is, the younger it is relative to dinosaurs lower in the sediments. Over time sediments form distinct stratigraphic beds that are called formations. For example, *Apatosaurus*, *Brontosaurus*, *Diplodocus*, *Barosaurus*, *Stegosaurus*, *Camptosaurus*, *Allosaurus*, and *Ornitholestes* are found in the Morrison Formation of western North America, which was laid down in the Late Jurassic, from 156 to 147 million years ago. Deposited largely by rivers over an area covering many states in the continental interior, the Morrison Formation is easily distinguished from the marine Sundance Formation lying immediately below as well as from the similarly terrestrial Cedar Mountain Formation above, which contains a very different set of dinosaurs. Because the Morrison was formed over millions of years, it can be subdivided into lower (older), middle, and upper (younger) levels. So a fossil found in the Sundance is older than one found in the Morrison, a dinosaur found in the lower Morrison is older than one found in the middle, and a dinosaur from the Cedar Mountain is younger still.

Geological time is divided into a hierarchical set of names. The Mesozoic is an era—preceded by the Paleozoic and followed by the Cenozoic—that contained the three progressively younger periods called the Triassic, Jurassic, and Cretaceous. These are then divided into Early, Middle, and Late, except that the Cretaceous is split only into Early and Late despite being considerably longer than the other two periods (this was not known when the division was made in the 1800s). The periods are further subdivided into stages. The Morrison Formation, for example, began to be deposited during the last part of the Oxfordian, continued through the entire Kimmeridgian, and the top part was formed at the beginning of the Tithonian.

The absolute age of recent fossils can be determined directly by radiocarbon dating. Dependent on the ratios of carbon isotopes, this method works only on bones and other specimens going back up to fifty thousand years, far short of the dinosaur era. Because it is not possible to directly date Mesozoic dinosaur remains, we must instead date the formations that the specific species are found in. This is viable because a given dinosaur species lasted only a few hundred thousand to a few million years.

The primary means of absolutely determining the age of dinosaur-bearing formations is radiometric dating. Developed by nuclear scientists, this method exploits the fact that radioactive elements decay in a very precise manner over time. The main nuclear transformations used are uranium to lead, potassium to argon, and one argon isotope to another argon isotope. This system requires the presence of volcanic deposits that initially set the nuclear clock. These deposits are usually in the form of ashfalls similar to the one deposited by Mount Saint Helens over neighboring states that leave a distinct layer in the sediments. Assume that one ashfall was deposited 144 million years ago, and another one higher in the sediments 141 million years ago. If a dinosaur is found in the deposits in between, then we know that the dinosaur lived between 144 and 141 million years ago. As the technology advances and the geological record is increasingly better known, radiometric dating is becoming increasingly precise. The further back in time one goes, the greater the margin of error, and the less exactly the sediments can be dated.

Volcanic deposits are often not available, and other methods of dating must be used. Doing so requires biostratigraphic correlation, which can in turn depend in part on the presence of "index fossils." Index fossils are organisms, usually marine invertebrates, that are known to have existed for only geologically brief periods of time, just a few million years at most. Assume a dinosaur species is from a formation that lacks datable volcanic deposits. Also assume that the formation grades into marine deposits laid down at the same time near its edge. The marine sediments contain small organisms that lasted for only a few million years in time. Somewhere else in the world, the same species of marine life was deposited in a marine formation that includes volcanic ashfalls that have been radiometrically dated to between 84 and 81 million years. We can then conclude that the dinosaur in the first formation is also 84 to 81 million years old.

A number of dinosaur-bearing formations lack both volcanic deposits and marine index fossils. It is not possible to accurately date the dinosaurs in these deposits. It is only possible to broadly correlate the level of development of the dinosaurs and other organisms in the formation with faunas and floras in better-dated formations, and this produces only approximate results. This situation is especially common in central Asia. The reliability of dating therefore varies. It can be very close to the actual value in formations that have been well studied and contain volcanic deposits; these can be placed in specific parts of a stage. At the other extreme are those formations that, because they lack the needed age determinants, and/or because they have not been sufficiently well examined, can only be said to date from the early, middle, or late portion of one of the periods, an error that can span well over 10 million years. North America currently has the most robust linkage of the geological time scale with its fossil dinosaurs of anywhere on Earth.

THE EVOLUTION OF DINOSAURS AND THEIR WORLD

Dinosaurs appeared in a world that was both ancient and surprisingly recent—it is a matter of perspective. The human view that the age of dinosaurs was remote in time is an illusion that results from our short life span. A galactic year, the time it takes our solar system to orbit the center of the galaxy, is 200 million years. Only one galactic year ago the dinosaurs had just appeared on planet Earth. When dinosaurs first appeared, our solar system was already well over 4 billion years old, and 95 percent of the history of our planet had already passed. A time traveler arriving on Earth when dinosaurs first appeared would have found it both comfortingly familiar and marvelously different from our time.

As the moon slowly spirals out from the Earth because of tidal drag, the length of each day grows. When dinosaurs first evolved, a day was about 22 hours and 45 minutes long, and the year had 385 days; when they went largely extinct, a day was up to 23 hours and over 30 minutes, and the year was down to 371 days. The moon would have looked a little larger and would have more strongly masked the sun during eclipses—there would have been none of the rare annular eclipses in which the moon is far enough away in its elliptical orbit that the sun rings the moon at maximum. The "man on the moon" leered down upon the dinosaur planet, but the prominent Tycho crater was not blasted into existence until toward the end of the Early Cretaceous. As the sun converts an increasing portion of its core from hydrogen into helium, it becomes hotter by nearly 10 percent every billion years, so the sun was about 2 percent cooler when dinosaurs first showed up and around a half percent cooler than it is now when most went extinct.

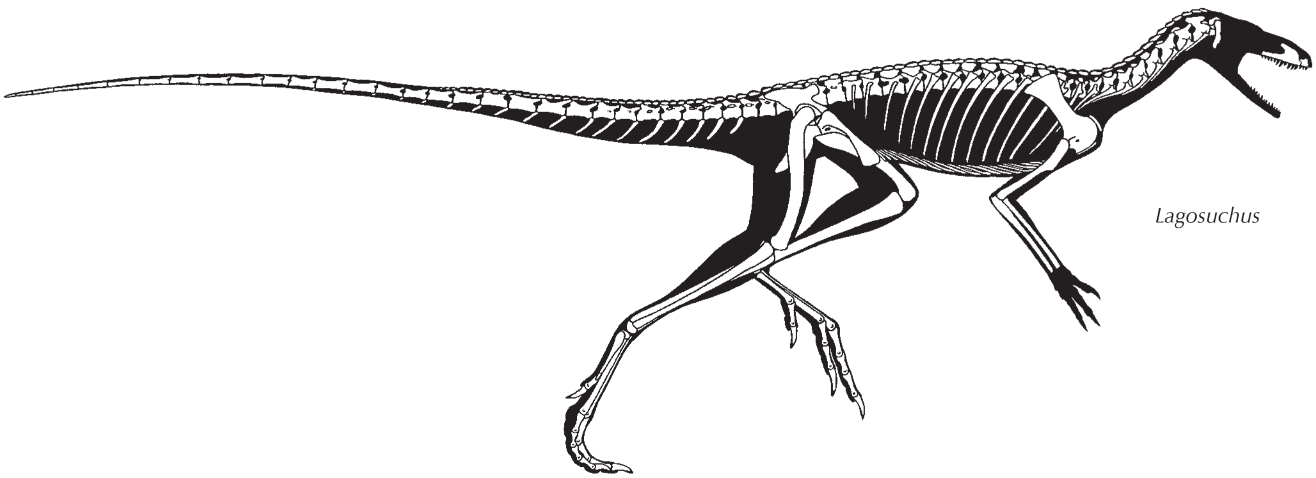
At the beginning of the great Paleozoic Era over half a billion years ago, the Cambrian Revolution saw the advent of complex, often hard-shelled organisms. Also appearing were the first, simple vertebrates. As the Paleozoic progressed, first plants and then animals, including tetrapod vertebrates, began to invade the land, which saw a brief Age of Amphibians in the late Mississippian followed by the classic Age of Reptiles in the Pennsylvanian and much of the Permian. By the last period in the Paleozoic, the Permian, the continents had joined together into the supercontinent Pangaea, which straddled the equator and stretched nearly to the poles north and south. With the majority of land far from the oceans, most terrestrial habitats were harshly semiarid, ranging from extra hot in the tropics to sometimes glacial at high latitudes. The major vertebrate groups had evolved by that time. Among synapsids, the mammal-like therapsids, some up to the size of rhinos, were the dominant large land animals in the Age of Therapsids of the Late Permian. These were apparently more energetic than reptiles, and those living in cold climates may have used fur to conserve heat. Toward the end of the period, the first archosaurs appeared. These low-slung, vaguely lizard-crocodilian creatures were a minor part of the global fauna. The conclusion of the Permian saw a massive extinction that has yet to be entirely explained and that, in many regards, exceeded the extinction that killed off the terrestrial dinosaurs 185 million years later.

At the beginning of the first period of the Mesozoic, the Triassic, the global fauna was severely denuded. As it recovered, the few remaining therapsids enjoyed a second evolutionary radiation and again became an important part of the wildlife. Again, they never became truly enormous or tall. This time they had competition, as the archosaurs also underwent an evolutionary explosion, first expressed as a wide variety of thecodonts, some of which reached a tonne in mass. One group evolved into aquatic, armored crocodile mimics. Others became armored land herbivores. Many were terrestrial predators that moved on erect legs achieved in a manner different from dinosaurs. The head of the femur did not turn inward; instead, the hip socket expanded over the femoral head until the shaft could be directed downward. Some of these erect-legged archosaurs were nearly bipedal. Others became toothless plant eaters. It is being realized that in many respects the Triassic thecodonts filled the lifestyle roles that would later be occupied by dinosaurs. Even so, these basal archosaurs never became gigantic or very tall. Also coming onto the scene were the crocodilians, the only group surviving today that reminds us what the archosaurs of the Triassic were like. Triassic crocodilians started out as small, long-legged, digitigrade land runners. Their sophisticated liver-pump lung systems may have evolved to help power a highly aerobic exercise ability. Crocodilians, like many of the thecodonts, had a very undinosaurian feature. Their ankles were complex, door-hinge-like joints in which a tuber projecting from one of the ankle bones helped increase the leverage of the muscles on the foot, rather as in mammals. At some time in the period, the membrane-winged, long-tailed pterosaurs evolved. Because pterosaurs had the same kind of simple-hinge ankle seen in dinosaurs, it has been suggested that the two groups are related. The energetic pterosaurs were insulated; we do not yet know whether other nondinosaurian archosaurs were also covered with thermal fibers, but the possibility is substantial.

In the Anisian and Ladinian, the two stages of the Middle Triassic, quite small predatory archosaurs appeared that exhibited many of the features of dinosaurs. Although the hip socket was still not internally open, the femoral head was turned inward, allowing the legs to operate in a vertical plane. The ankle was a simple hinge. The skull was lightly constructed. At first known only from South America, these protodinosaurs have since been found on other continents. These early dinosaurian forms would survive only until the Norian. Protodinosaurs show that dinosaurs started out as little creatures; they did not descend from the big basal archosaurs.

From small things big things can evolve, and very quickly. In the Carnian stage of the Late Triassic the fairly large-bodied, small-hipped, four-toed herrerasaur theropods were on the global stage. These bipeds dwelled in a world still dominated by complex-ankled archosaurs and would not last beyond the Norian or maybe the Rhaetian stage, perhaps because these early dinosaurs did not have an aerobic capacity high enough to vie with their new competitors. The Norian saw the appearance of the great group that is still with us, the bird-footed avepod theropods, whose large hips and beginnings of the avian-type respiratory system imply a further improvement in aerobic performance and thermoregulation. At about the same time, the first members of one of the grand groups of herbivorous dinosaurs are first recorded in the fossil record, the small-hipped, semibipedal prosauropods, followed almost immediately by the quadrupedal and bigger-hipped sauropods. These new dinosaurs gave thecodonts increasing competition as they rapidly expanded in diversity as well as size. Just 15 or 20 million years after the evolution of the first little protodinosaurs, prosauropods and sauropods weighing 2 tonnes had developed. In only another 10 million years, sauropods as big as elephants, the first truly gigantic land animals, were extant. These long-necked dinosaurs were also the first herbivores able to browse at high levels, many meters above the ground. Dinosaurs were showing the ability to evolve enormous dimensions and bulk on land, an attribute otherwise seen only among mammals. In the Carnian the first of the beaked herbivorous ornithischians arrived. These little semibipeds were not common, and they, as well as small prosauropods, may have dug burrows as refuges from a predator-filled world. By the last stage of the Triassic the saurischian dinosaurs were becoming the ascendant land animals, although they still lived among thecodonts and some therapsids. From the latter, at this time, evolved the first mammals. Mammals and dinosaurs have, therefore, shared the planet for over 200 million years—and for 140 million of those years, mammals would remain small.

Because animals could wander over the entire supercontinent with little hindrance from big bodies of water, faunas



Lagosuchus

Silesaurus

Protodinosaurs

tended to exhibit little difference from one region to another. And with the continents still collected together, the climatic conditions over most of the supercontinent remained harsh. It was the greenhouse world that would prevail through the Mesozoic. The carbon dioxide level was two to ten times higher than it is currently, boosting temperatures to such highs—despite the slightly cooler sun of those times—that even the polar regions were fairly warm in winter. The low level of tectonic activity meant there were few tall mountain ranges to capture rain or interior seaways to provide moisture. Hence, there were great deserts, and most of the vegetated lands were seasonally semiarid, but forests were located in the few regions of heavy rainfall and groundwater created by climatic zones and rising uplands. It appears that the tropical latitudes were so hot and dry that the larger dinosaurs, with their high energy budgets, could not dwell near the equator and were restricted to the cooler, wetter, higher latitudes. The flora was in many respects fairly modern and included many plants we would be familiar with. Wet areas along watercourses were the domain of rushes and horsetails. Some ferns also favored wet areas and shaded forest floors. Other ferns grew in open areas that were dry most of the year, flourishing during the brief rainy season. Large parts of the world may have been covered by fern prairies, comparable to the grasslands and shrublands of today. Tree ferns were common in wetter areas. Even more abundant were the fernlike or palmlike cycadeoids, similar to the cycads that still inhabit the tropics. Taller trees included water-loving ginkgoids, of which the maidenhair tree is the sole—and, until widely planted in urban areas, the nearly extinct—survivor. Dominant among plants were conifers, most of which at that time had broad leaves rather than needles. Some of the conifers were giants rivaling the colossal trees of today, such as those that formed the famed Petrified Forest of Arizona. Flowering plants were completely absent.

The end of the Triassic about 200 million years ago saw another extinction event whose cause is obscure. A giant impact occurred in southeastern Canada, but it was millions of years before the extinction. The thecodonts and therapsids suffered the most: the former were wiped out, and only scarce remnants of the latter survived along with mammal relatives. In contrast, crocodilians, pterosaurs, and especially dinosaurs sailed through the crisis into the Early Jurassic with little disruption. Avepod theropods such as *Coelophysis* remained common and little changed, as did prosauropods. Sauropods just got bigger. For the rest of the Mesozoic, dinosaurs would enjoy almost total dominance on land except for some semiterrestrial crocodilians; there simply were no competitors above a few kilograms in weight. Such extreme superiority was unique in Earth's history. The Jurassic and Cretaceous combined were the Age of Dinosaurs.

The Late Triassic *Coelophysis*

As the Jurassic progressed, the prosauropods appear to have been unable to compete with their more sophisticated sauropod relatives and were gone by the end of the Early Jurassic. The larger hip muscles and the beginnings of a birdlike respiratory system suggest that sauropods had the higher aerobic capacity and higher-pressure circulatory system needed to achieve truly great height and bulk. Although some theropods were getting moderately large, the much more gigantic sauropods enjoyed a period of relative immunity from attack. Ornithischians remained uncommon, and one group was the first set of dinosaurs to develop armor protection. Another group of ornithischians was the small, chisel-toothed, semibipedal heterodontosaurs, which established that fiber coverings had evolved in some small dinosaurs by this time if not earlier. On the continents, crocodilians remained small and fully or semiterrestrial, while other groups became marine giants.

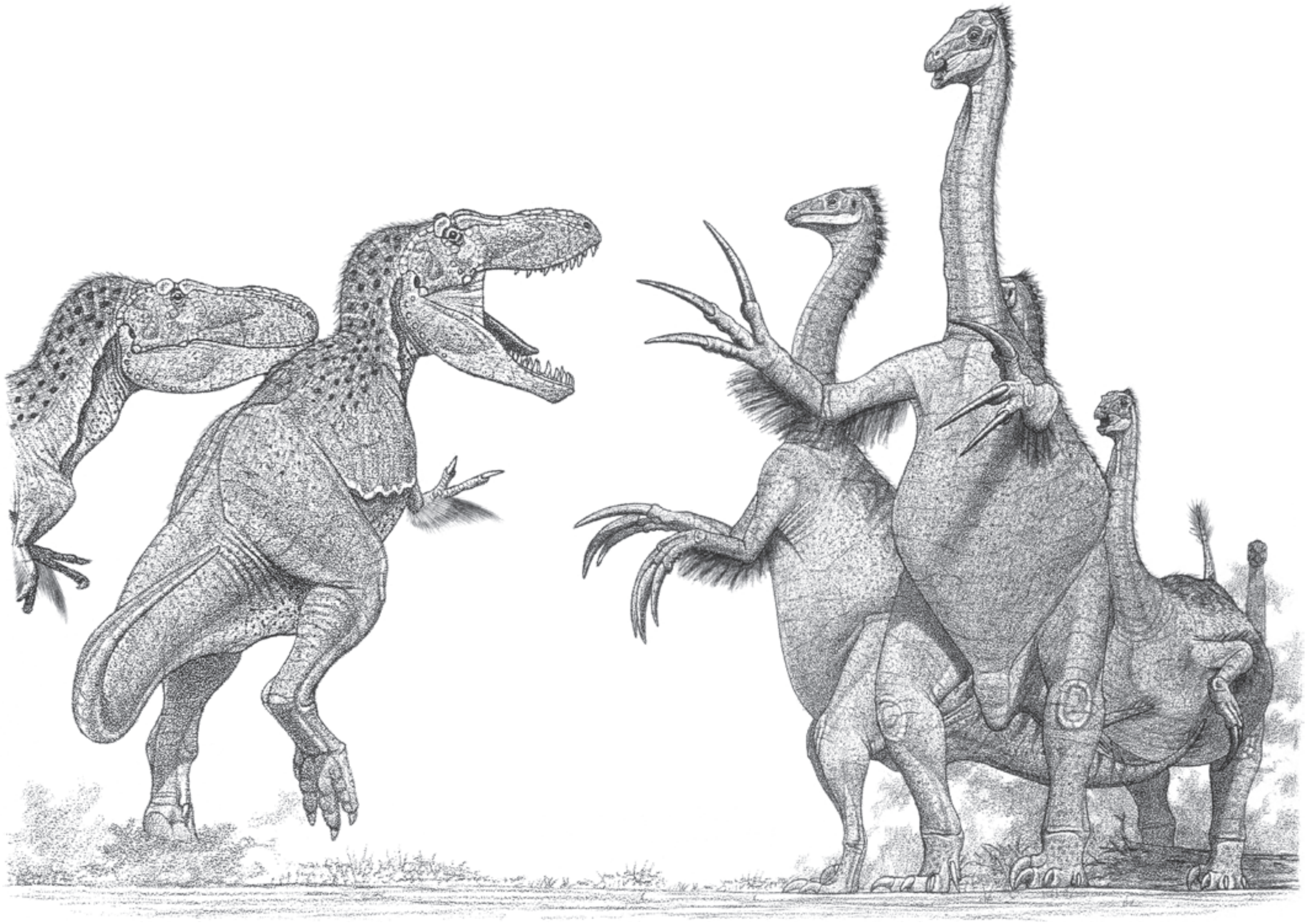
Partly splitting Pangaea into northern Laurasia and southern Gondwanaland like a marine wedge was the great Tethys tropical ocean, the only surviving remnant of which is the Mediterranean. Farther west, the supercontinent was beginning to break up, creating African-style rift valleys along today's Eastern Seaboard of North America that presaged the opening of the Atlantic. More importantly for dinosaur faunas, the increased tectonic activity in the continent-bearing conveyor belt formed by the mantle caused the ocean floors to lift up, spilling the oceans onto the continents in the form of shallow seaways that began to isolate different regions from one another, encouraging the evolution of a more diverse global wildlife. The expansion of so much water onto the continents also raised rainfall levels, although most habitats remained seasonally semiarid. The moving land masses also produced more mountains able to squeeze rain out of the atmosphere.

Beginning 175 million years ago, the Middle Jurassic began the Age of Sauropods, whose increasingly sophisticated respiratory and circulatory systems allowed them to match medium-sized whales in bulk and trees in height. Sauropods thrived even in dry habitats by feeding on the forests that lined watercourses as well as the fern prairies in the wet season. In China, partly isolated by seaways, some sauropods evolved slender necks so long that they could feed 10 meters (over 30 feet) high. A few sauropods had tail spikes or clubs. Also appearing were the first small, armored stegosaur ornithischians that also introduced tail spikes. Even smaller were the little ornithopods, the beginnings of a group of ornithischians whose respiratory systems—which may have paralleled those of mammals—and dental batteries gave them great evolutionary potential. Although the increasingly sophisticated tetanuran, avetheropod, and coelurosaur theropods evolved and featured highly developed avian-type respiratory systems, for reasons that are obscure, they continued to fail to produce true giants. There is new evidence that flowering plants were present by the middle of the Jurassic, but even if so they were not yet common.

The Late Jurassic, which began 160 million years ago, was the apogee of two herbivorous dinosaur groups, the sauropods and the stegosaurs. Sauropods, which included haplocanthosaurs, mamenchisaurs, dicraeosaurs, diplodocines, apatosaurines, camarasaurs, and the first titanosaurs, would never again be so diverse. Some neosauropods rapidly enlarged to 50 to 75 tonnes, and a few may have greatly exceeded 100 tonnes, rivaling the biggest baleen whales. The tallest sauropods could feed over 20 meters (70 feet) high. But it was a time of growing danger for the sauropods: theropods had finally evolved hippo-sized yangchuanosaurs and allosaurs that could tackle the colossal herbivores. Meanwhile, some sauropods isolated on islands underwent dwarfing to rhino size to better accommodate to the limited resources (the same would happen to elephants and hippos). The rhino- and sometimes elephant-sized stegosaurs were at their most diverse. But the future of the other group of big armored dinosaurs, the short-legged ankylosaurs, was beginning to develop. Also entering the fauna were the first fairly large ornithopods, sporting thumb spikes. Asia saw the development of small semibipedal ceratopsians.

The still-small ancestors of tyrannosaurs seem to have been developing at this time, and assorted gracile maniraptor coelurosaurs were numerous. Also present by the Late Jurassic were the curious alvarezsaurs, whose stout and short arms and hands were adapted for breaking into insect nests. But it is the advent of the highly birdlike and probably partly arboreal aveairfoilans at the end of the mid-Jurassic going into the late part of the period that was a major event. Dinosaur flight appears to have come in two versions. One experiment was the bat-winged scansoriopterygids of Asia; these apparently soon disappeared, perhaps because of competition from the bird-winged aveairfoilans. The Chinese deinonychosaur *Anchiornis* is the earliest dinosaur known to have had large feathers on its arms, and on its legs too. Because the moderately long, symmetrical feathers were not proper airfoils despite the great length of the arms, this apparent climber may be the first example of a reduction of flight abilities from an ancestor with superior aerial prowess. A few million years later, when Europe was still a nearshore

The Late Jurassic *Giraffatitan* and *Dicraeosaurus*



The Late Cretaceous *Tyrannosaurus* and *Therizinosaurus*

extension of northeastern North America, the first "bird," the deinonychosaur *Archaeopteryx*, was extant. Preserved in lagoonal deposits on the northwestern edge of the then great Tethys Ocean, it had a combination of very large arms and long, asymmetrical wing feathers indicating that it was part of the process of developing the early stages of powered flight. The advent of the little aveairfoilans also heralded the first major increase in dinosaurian mental powers, as brain size and complexity rose to the lower avian level. Pterosaurs, which retained smaller brains, remained small bodied, and most still had long tails. Although some crocodilians were still small runners, the kind of highly amphibious crocodilians of the sort we are familiar with were appearing. Their liver-pump lung systems readapted into buoyancy control devices. Although small, mammals were undergoing extensive evolution in the Jurassic. Many were insectivorous or herbivorous climbers, but some were burrowers, and others had become freshwater-loving swimmers weighing a few kilograms.

During the Middle and Late Jurassic, carbon dioxide levels were incredibly high, with the gas making up between 5 percent and 10 percent of the atmosphere. As the Jurassic and the Age of Sauropods ended, the incipient North Atlantic was about as large as today's Mediterranean. Vegetation had not yet changed dramatically from the Triassic. Wetter areas were dominated by conifers similar to cypress. A widespread and diverse conifer group of the time was the araucarians. Some appear to have evolved a classic umbrella shape in which most of the adult trunk was as bare of foliage as a telephone pole, with all of the branches concentrated at the top. Still seen in a few South American examples, this odd shape may have evolved as a means of escaping browsing by the sauropods, which should have had a profound impact on floral landscapes as they heavily browsed and wrecked trees to an extent that probably exceeded that of elephants. What happened to the fauna at the end of the Jurassic is not well understood because of a lack of deposits. Some researchers think that there was a major extinction, but others disagree.

The Cretaceous began 145 million years ago. This period would see an explosion of dinosaur evolution that surpassed all that had gone before as the continents continued to split, the south Atlantic began to open, and seaways crisscrossed the continents. Greenhouse conditions became less extreme as carbon dioxide levels gradually edged downward, although never down to the modern preindustrial level. Early in the Cretaceous, the warm Arctic oceans kept conditions up there balmy even in the winter. At the other pole, continental conditions rendered winters frigid enough to form permafrost. General global conditions were a little wetter than they were earlier in the Mesozoic, but seasonal aridity remained the rule in most places, and true rain forests continued to be scarce at best.

Sauropods remained abundant and often enormous, but they were less diverse than before, as a few small-bodied, short-necked diplodocoids—some with broad, square-ended mouths specialized for grazing—tall brachiosaurs, and especially the broad-bellied titanosaurs predominated.

To a fair extent the Cretaceous was the Age of Ornithischians. Ornithopods small and especially large flourished. Thumb-spiked iguanodonts soon became common herbivores in the Northern Hemisphere. Their well-developed dental batteries may have been a key to their success. A few evolved tall sails formed by their vertebral spines. Until recently it was thought that the heterodontosaur clade had failed well back in the Jurassic, but we now know that they made it into at least the early Cretaceous in Asia with little change in form. Among ceratopsians, the small Asian chisel-toothed psittacosaurs first proliferated, and their relatives, the big-headed protoceratopsids, appeared in the same region. So did the first of the dome-headed pachycephalosaurs. Stegosaurs, however, soon departed the scene, the final major dinosaur group to become totally extinct since the prosauropods. This reveals that over time the dinosaurs tended to add new groups without losing the old ones, building up their diversity over the Mesozoic. In the place of stegosaurs, the low-slung and extremely fat-bellied armored ankylosaurs became a major portion of the global fauna, their plates and spikes providing protection from the big Laurasian allosauroids and the snub-nosed, short-armed abelisaurs in Gondwana. Another group of giant theropods, the croc-snouted spinosaurs, apparently adapted to catch fish as part of their diet. Bone isotopes indicate that spinosaurs were semiaquatic like hippos. Some of them also evolved great sail backs.

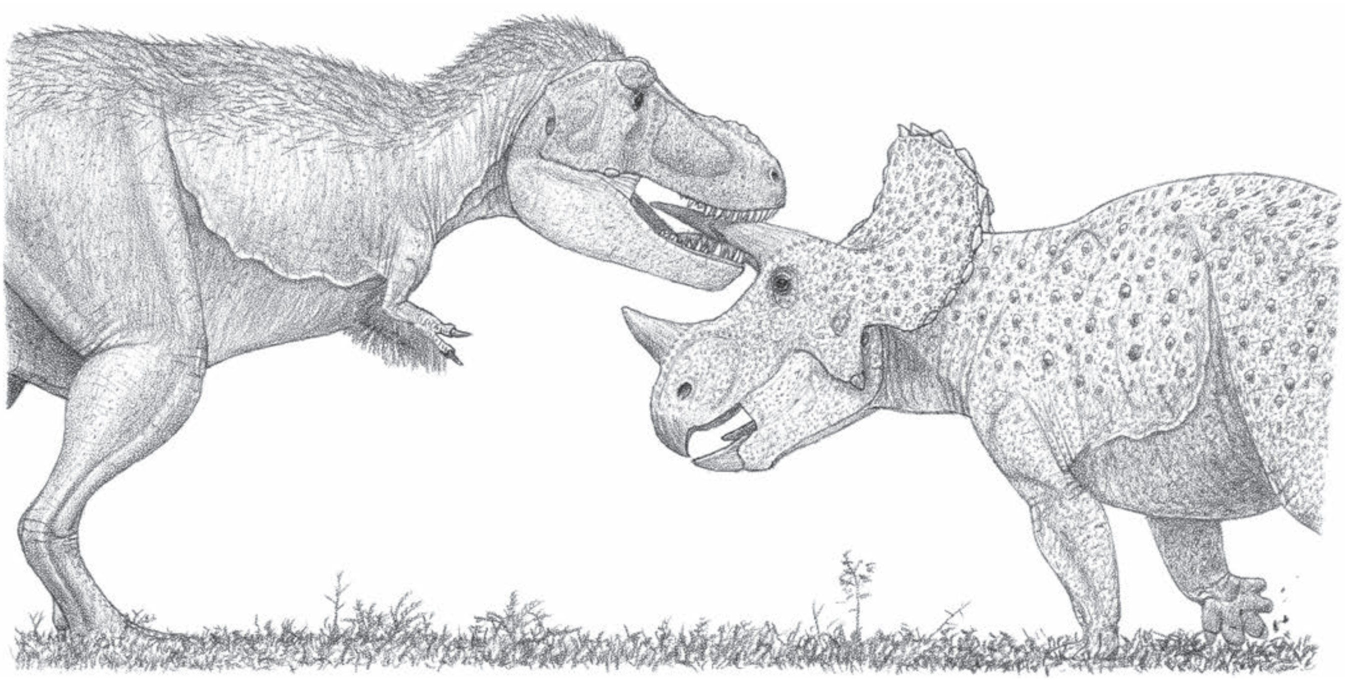
It was among the smaller theropods that dinosaur evolution really went wild in the Early Cretaceous. The first of the ostrich-mimicking ornithomimids were present, as were the initial, not yet titantic, tyrannosaurs with similarly long running legs and reduced arms. But the focus of events was among the nearly avian aveairfoilans. As revealed by the spectacular lake deposits of northeastern China, deinonychosaurs developed into an array of flying and flightless forms, with the latter possibly secondarily flightless descendants of the fliers. The famous sickle-clawed dromaeosaurs appear to have begun as small aerialists with two sets of wings, the normal ones on the arms and an equally large set on the hind legs. From these appear to have evolved bigger terrestrial dromaeosaurs that hunted large game. The other major sickle-clawed deinonychosaur group, the more lightly built and swifter-running troodonts, also thrived.

At the same time, birds themselves not only descended from deinonychosaur dinosaurs, the Chinese deposits show they had already undergone a spectacular evolutionary radiation by 125 million years ago. Some retained teeth; others were toothless. Some had long tails; most did not. None were especially large. Among these early birds were the toothed, long-skulled, and long-tailed herbivorous jeholornithiformes. It is possible that they were the ancestors of the enigmatic, potbellied, land-bound therizinosaur dinosaurs. The short-tailed, deep-beaked omnivoropterygid birds bear a striking resemblance to the caudipterygid and protarchaeopterygid oviraptorosaurs from the same formations. It is possible that the short-tailed oviraptorosaurs were another group of secondarily flightless dinosaur-birds, ones more advanced than the archaeopterygian-dromaeosaur-troodont deinonychosaurs, and the therizinosaurs. The conventional view held by most researchers is that flightless therizinosaurs and oviraptorosaurs happened to be convergent with the flying jeholornithiformes and omnivoropterygids, respectively.

Pterosaurs, most of them now short tailed and consequently more dynamic fliers, were becoming large as they met increasing competition from birds. Also fast increasing in size were the freshwater crocodilians, making them an increasing threat for dinosaurs coming to water to drink or for other purposes. Some large crocodilians were semiterrestrial and able to attack big dinosaurs on land as well as in the water. Still scampering about were a few small running crocodilians. Some carnivorous mammals were big enough, about a dozen kilograms, to catch and consume the smallest dinosaurs and their babies. Even gliding mammals had evolved by this time.

During the late Early Cretaceous a major evolutionary event occurred, one that probably encouraged the rapid evolution of dinosaurs. Flowering plants began to become an important portion of the global flora. The first examples were small shrubs growing along shifting watercourses where their ability to rapidly colonize new territory was an advantage. Others were more fully aquatic, including water lilies. Their flowers were small and simple. The fast growth and strong recovery potential of flowering plants may have encouraged the development of low-browsing ankylosaurs and ornithopods. Conversely, the browsing pressure of dinosaurs may have been a driving force behind the evolution of the fast-spreading and fast-growing new plants. Also appearing about this time were South American conifers with monkey-puzzle foliage, their umbrella shape encouraged by the ever-hungry sauropods.

In the Late Cretaceous, which began 100 million years ago, the continental breakup was well under way, with interior seaways often covering vast tracts of land. As carbon dioxide levels continued to drop, the dark Arctic winters became cold enough to match the conditions seen in today's high northern forests, and glaciers crept down high-latitude mountains. Mammals were increasingly modern, and small. Pterosaurs, marine and terrestrial, became gigantic to a degree that stretches credulity. Oceanic pteranodonts had wings stretching 8 meters (over 25 feet). Toward the end of the Cretaceous, the freshwater-loving



***Tyrannosaurus* biting off the horn of a *Triceratops*, based on a fossil of the latter**

azhdarchids sported wings of 11 meters (over 35 feet) and outweighed ostriches. Small running crocodilians remained extant, and a few even became herbivorous. As for the conventional freshwater crocodilians, in some locales they become colossi up to 12 meters (close to 40 feet) long and approaching 10 tonnes, as large as the biggest flesh-eating theropods. Although these monsters fed mainly on fish and smaller tetrapods, they posed a real threat to all but the largest dinosaurs. The hazard should not be exaggerated, however, because these supercrocs do not appear to have been very numerous in many locations and were absent at higher latitudes. Even so, their existence may have discouraged the evolution of highly aquatic dinosaurs.

Although sauropods soon became limited to the titanosaurs, they diversified and proliferated across most of the globe, being especially diverse in the Southern Hemisphere, wrapping up the 150 million years that made them the most successful herbivore group in Earth's history. Sauropods disappeared from North America for part of the Late Cretaceous, only to reappear in the drier regions toward the end. Some sauropods were armored; this may have been a means to protect the juveniles against the increasing threat posed by a growing assortment of predators. A few small titanosaurs had the short necks and square, broad mouths suited for grazing. Others were titanic, exceeding 50 and perhaps 100 tonnes up to the end of the dinosaur era. These were subject to attack from abelisaur and allosauroid theropods, some matching bull elephants in bulk. Perhaps even larger were the African sail-backed spinosaurs of the early Late Cretaceous; unlike the abelisaurs and allosauroids, this group did not make it to the end of the Mesozoic.

The ultrawide-bodied ankylosaurs continued their success, especially in the Northern Hemisphere. One group of the armored herbivores developed tail clubs with which to deter and if necessary damage their enemies, as well as settle breeding and perhaps feeding disputes within the species. The iguanodonts faded from the scene to be replaced by their descendants, the duck-billed hadrosaurs, which evolved the most complex grinding dental batteries among dinosaurs and often used elaborate head crests to identify the variety of species. The most common herbivores in much of the Northern Hemisphere, hadrosaurs may have been adapted in part to browse on the herbaceous shrubs and ground cover that were beginning to replace the fern prairies as well as to invade forest floors. Small ornithopods, not all that different from the bipedal ornithischians that had appeared back near the origins of the dinosaurs, continued to dwell over much of the globe. In the Northern Hemisphere the protoceratopsids, small in body and big in head, were common in many locales. It was from this stock that some of the most spectacular dinosaurs evolved—the rhino- and elephant-sized ceratopsids whose oversized heads sported horns, neck frills, great parrot-like beaks, and slicing dental batteries. These remarkable dinosaurs flourished for just the last 15 million years of the dinosaur era, limited largely to the modest-sized stretch of North America that lay west of the interior seaway; for some reason their presence in Asia was very limited.

Birds, some still toothed, continued to thrive. One group of oceanic birds lost flight to the point that they evolved into fully marine divers. By the late Cretaceous the classic short-armed coelurosaurs were no longer extant. The small predatory theropods consisted of the intelligent and sickle-clawed swift troodonts and leaping dromaeosaurs, some of which were still able to fly. Also successful were the short-tailed nonpredatory aveairfoilans, those being the deep-headed omnivorous oviraptorosaurs, many exhibiting dramatic head crests, as well as the small-headed, big-clawed herbivorous therizinosaurs. In both groups some species became quite large, as did some ornithomimosaurs. But among the latter group the long- and slender-legged ornithomimids became perhaps the fastest of all dinosaurs, although they were closely matched by the colonial insect-eating alvarezsaurs.

Culminating the over 150 million years of theropod history were the great tyrannosaurids, the most sophisticated and powerful of the gigantic predators. The classic great tyrannosaurids came into existence only some 15 million years before the end of the Mesozoic and were limited to Asia and North America. Apparently they wandered, along with other theropods, hadrosaurs, and ankylosaurs, across the subpolar Bering land bridge, where some became specialized for the winter climate. In North America a size race occurred as tyrannosaurids, ceratopsids, ankylosaurids, and pachycephalosaurids reached unprecedented sizes for their groups in the final few million years of the Cretaceous, resulting in the classic *Tyrannosaurus*, *Triceratops*, *Ankylosaurus*, and *Pachycephalosaurus* fauna; the ornithomimids got bigger too. This may have been the result of a predator-prey arms race, or expansion of the resource base as the retreating interior seaway linked the eastern and western halves of the continent into a larger land area, or a combination of both. It is interesting that the hadrosaurs did not get bigger—some earlier edmontosaurs were if anything larger than those that followed, some of the latter being well adapted for grazing. This pattern indicates that the enormous size and firepower of the American *Tyrannosaurus* was a specialization for hunting the equally oversized contemporary horned dinosaurs rather than just dispatching the easier-to-kill edmontosaurs. Nor did the armored nodosaurids enlarge at this time.

By the end of the Cretaceous the continents had moved far enough that the world was beginning to assume its modern configuration. At the terminus of the period a burst of uplift and mountain building had helped drain much of the seaways. Flowering plants were fast becoming an ever more important part of the flora, and the first hardwood trees—among them the plane tree commonly planted in cities—evolved near the end of the period and were evolving into the first large hardwood trees. Conifers remained dominant, however, among them the deciduous, moisture-dependent dawn redwoods that barely survived to modern times. Also common were the classic redwoods, which reached towering heights as they do today. In South America the browsing pressure of the towering titanosaurs may have continued to encourage the evolution of the umbrella-topped monkey-puzzle araucarians. Classic rain forests, however, still did not exist. Grasses had evolved: they tended to be water-loving forms and did not yet form dry grassland prairies.

Then things went catastrophically wrong.

EXTINCTION

The mass extinction at the end of the Mesozoic is generally seen as the second most extensive in Earth's history, after the one that ended the Paleozoic. However, the earlier extinction did not entirely exterminate the major groups of large land animals. At the end of the Cretaceous all nonavian dinosaurs, the only major land animals, were lost, leaving only flying birds as survivors of the group. Among the birds, all the toothed forms, plus a major Mesozoic bird branch, the enantiornithines, as well as the flightless birds of the time, were also destroyed. So were the last of the superpterosaurs and the most gigantic of the crocodilians.

It is difficult to exaggerate how remarkable the loss of the dinosaurs was. If dinosaurs had repeatedly suffered the elimination of major groups and experienced occasional diversity squeezes in which the Dinosauria was reduced to a much smaller collection that then underwent another evolutionary radiation until the next squeeze, then their final loss would not be so surprising. But the opposite is the case. A group that had thrived for over 150 million years over the entire globe, rarely suffering the destruction of a major group and usually building up diversity in form and species over time as they evolved into an increasingly sophisticated group, was in short order completely expunged. The small dinosaurs went with the large ones, predators along with herbivores and omnivores, and intelligent ones along with those with reptilian brains. It is especially notable that even the gigantic dinosaurs did not suffer repeated extinction events. Sauropods were always a diverse and vital group for almost the entire reign of dinosaurs. The same was true for giant theropods once they appeared, as well as ankylosaurs and the iguanodonts/hadrosaurs. Only the stegosaurs had faded away well into the dinosaur era. In contrast, many of the groups of titanic mammals appeared, flourished relatively briefly, and then went extinct. Dinosaurs appear to have been highly resistant to large-scale extinction. Rendering their elimination still more remarkable is that one group of dinosaurs, the birds, did survive, as well as aquatic crocodilians, lizards, snakes—the latter had evolved by the Late Cretaceous—amphibians, and mammals that proved able to weather the same crisis.

It has been argued that dinosaurs were showing signs of being in trouble in the last few million years before the final extinction. Whether they were in decline has been difficult to verify or refute even in those few locations where the last stage of the dinosaur era was recorded in the geological record, such as western North America. Even if true, the decline was at most only modest. At the Cretaceous/Paleocene (K/Pg), formerly the Cretaceous/Tertiary (K/T), boundary, the total population of juveniles and adult dinosaurs should have roughly matched those of similar-sized land mammals before the advent of humans, numbering in the billions and spread among many dozens or a few hundred species on all continents and many islands.

A changing climate has often been offered as the cause of the dinosaurs' demise. But the climatic shifts at the end of the Cretaceous were neither strong nor greater than those already seen in the Mesozoic. And dinosaurs inhabited climates ranging from tropical deserts to icy winters, so yet another change in the weather should not have posed such a lethal problem. If anything, reptiles should have been more affected. The rise of the flowering plants has been suggested to have adversely impacted dinosaurs, but the increase in food sources that the fast-growing seed- and fruit-producing plants provided appears to have been so much to the dinosaurs' benefit that it spurred the evolution of late Mesozoic dinosaurs. Mammals consuming dinosaur eggs are another proposed agent. But dinosaurs had been losing eggs to mammals for nearly 150 million years, and so had reptiles and birds without long-term ill effects. The spread of diseases as retreating seaways allowed once-isolated dinosaur faunas to intermix is not sufficient because of their prior failure to crash the dinosaur population, which was too diverse to be destroyed by one or a few diseases and which would have developed resistance and recovered its numbers. Also unexplained is why other animals survived.

The solar system is a shooting gallery full of large rogue asteroids and comets that can create immense destruction. There is widespread agreement that the K/P extinction was caused largely or entirely by the impact of at least one meteorite, a mountain-sized object that formed a crater 180 km (over 100 miles) across, located on the Yucatán Peninsula of Mexico. The evidence strongly supports the object being an asteroid rather than a comet, so speculations that a perturbation of the Oort cloud as the solar system traveled through the galaxy and its dark matter are at best problematic. The explosion of 100 teratons surpassed the power of the largest H-bomb detonation by a factor of 20 million and dwarfed the total firepower of the combined nuclear arsenals at the height of the Cold War. The blast and heat generated by the explosion wiped out the fauna in the surrounding vicinity, and enormous tsunamis cleared off many coastlines. On a wider scale, the cloud of high-velocity debris ejected into space glowed hot as it reentered the atmosphere in the hours after the impact, creating a global pyrosphere that may have been searing enough to bake animals to death as it ignited planetary wildfires. The initial disaster would have been followed by a solid dust pall that plunged the entire world into a dark, cold winter lasting for years, combined with severe air pollution and acid rain. As the aerial particulates settled, the climate then flipped as enormous amounts of carbon dioxide—released when the impact hit a tropical marine carbonate platform—created an extreme greenhouse effect that baked the planet for many thousands of years. Such a combination of agents appears to solve the mystery of the annihilation of the dinosaurs. Even so, some problems remain.

It is not certain whether the pyrosphere was as universally lethal as some estimate. Even if it was, heavy storms covering a small percentage of the land surface should have shielded a few million square kilometers, equal in total to the size of India, creating scattered refugia. In other locations dinosaurs that happened to be in burrows, caves, and deep gorges, as well as in water, should have survived the pyrosphere. So should many of the eggs buried in covered nests. Birds and amphibians, which are highly sensitive to environmental toxins, survived the acid rain and pollution. Because dinosaurs were rapidly reproducing animals whose self-feeding young could survive without the care of the parents, at least some dinosaurs should have made it through the crisis, as did some other animals, recolonizing the planet as it recovered.

Massive volcanism occurred at the end of the Cretaceous as enormous lava flows covered 1.5 million square kilometers, a third of the Indian subcontinent. It has been proposed that the massive air pollution produced from the repeated supereruptions damaged the global ecosystem so severely in so many ways that dinosaur populations collapsed in a series of stages, perhaps spanning tens or hundreds of thousands of years. This hypothesis is intriguing because extreme volcanic activity also occurred during the great Permo-Triassic extinction; those eruptions were in Siberia. Although the K/Pg Deccan Traps were being extruded before the Yucatán impact, evidence indicates that the latter—which generated earthquakes of magnitude 9 over most of the globe (11 at the impact site)—greatly accelerated the frequency and scale of the eruptions. If this is correct, then the impact was responsible for the extinction not just via its immediate, short-term effects, but by sparking a level of extended supervolcanism that prevented the recovery of dinosaurs. It is also possible that the Yucatán impactor was part of an asteroid set that hit the planet repeatedly, further damaging the biosphere. Even so, the combined impact/volcanic hypothesis does not fully explain why dinosaurs failed to survive problems that other continental animals did.

Although extraterrestrial impact(s), perhaps indirectly linked with volcanism, is the leading explanation, the environmental mechanisms that destroyed all of the nonflying dinosaurs while leaving many birds and other animals behind remain incompletely understood.

AFTER THE AGE OF DINOSAURS

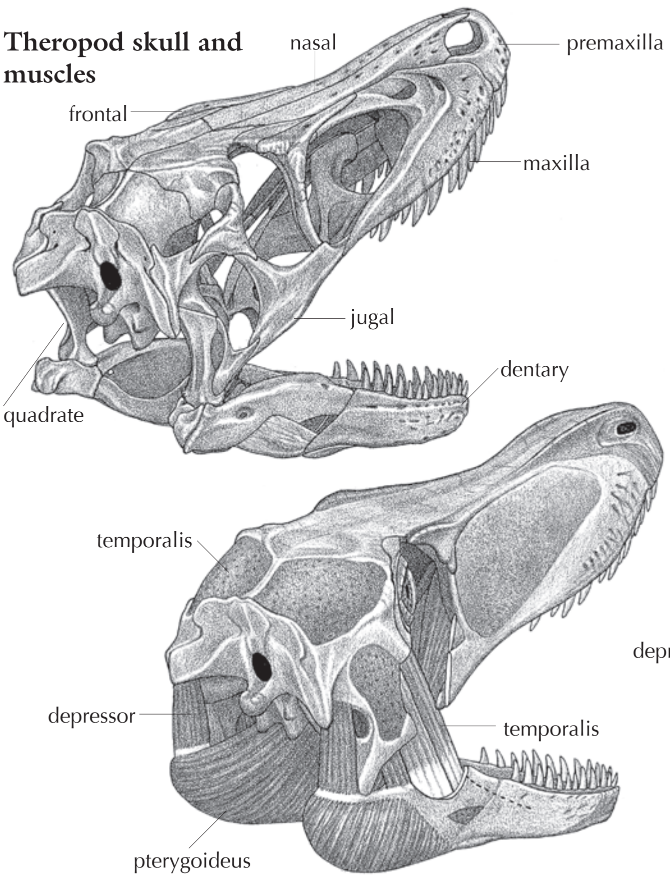
Perhaps because trees were freed from chronic assault by sauropods, dense forests, including rain forests, finally appeared. After the extinction of the nonavian dinosaurs, there were no large land animals, and only large freshwater crocodilians could make a living feeding on fish. The loss of dinosaurs led to a second, brief Age of Reptiles as superboa snakes as long as the biggest theropods and weighing over a tonne quickly evolved in the tropics. Their main prey was probably a diverse array of crocodilians, some semiterrestrial, as well as mammals, which were also swiftly expanding in size. By 40 million years ago, about 25 million years after the termination of large dinosaurs, some land and marine mammals were evolving into giants rivaling the latter. Among the survivors of the Dinosauria, a number of birds lost flight and soon became large land runners and marine swimmers. But the main story of Cenozoic dinosaurs has been their governance of the daylight skies, while the night has been dominated by the mammalian fliers, the bats. The greatest success story of modern flying dinosaurs? The marvelous diversity and numbers of the little but sophisticated passerine songbirds that fill field guides.

BIOLOGY

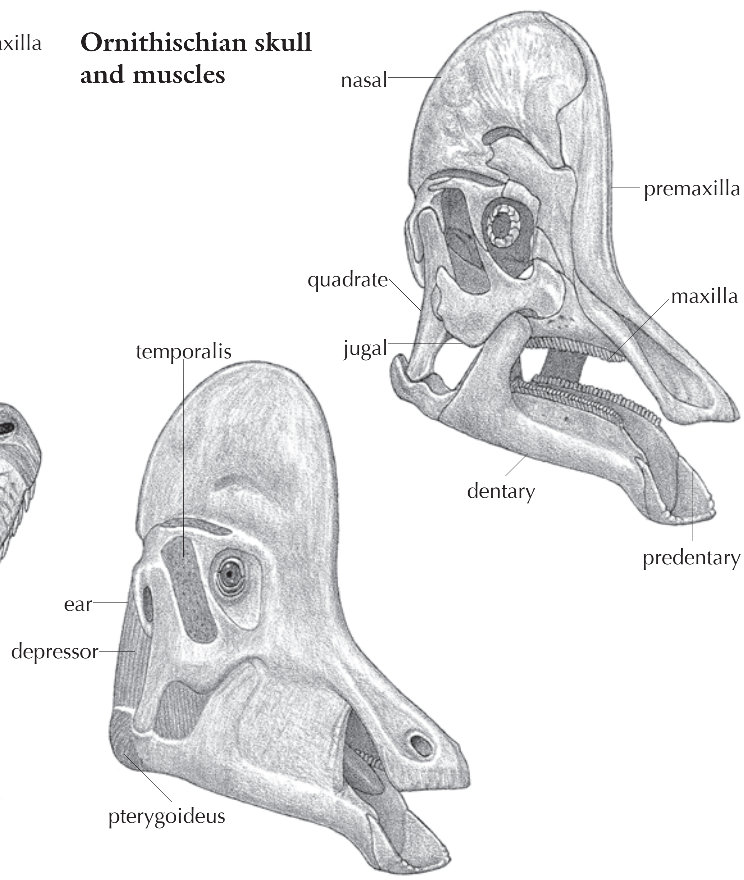
General Anatomy

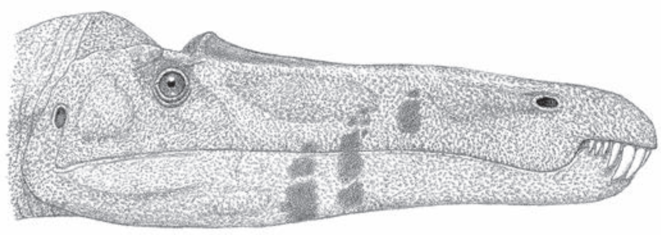
Dinosaur heads ranged from remarkably delicately constructed to massively built. In all examples the nasal passages or the sinuses or both were very well developed, a feature common to archosaurs in general. Many dinosaurs retained a large opening immediately in front of the orbits; in others this opening was almost entirely closed off. Unlike mammals with their extensive facial musculature, dinosaurs, like reptiles and birds, lacked facial muscles, so the skin was directly appressed to the skull. This feature makes dinosaur heads easier to restore than those of mammals. The external nares are always located far forward in the nasal depression no matter how far back on the skull the nasal openings extend. In some sauropods the nasal openings are set far back on the skull, above the eye sockets. It was once thought that this allowed these dinosaurs to snorkel when submerged. More recently it has been suggested that the retracted nostrils evolved to avoid irritation from needles as sauropods fed on conifers. Most conifers at that time, however, had soft leaves. In any case, the fleshy nostrils extended far forward so that the external nares were in the normal position near the tip of the snout. There is no anatomical evidence that any dinosaur had a proboscis. The skin covering the large openings in front of the orbits of many dinosaurs probably bulged gently outward. Jaw muscles likewise bulged gently out of the skull openings aft of the eye sockets.

Theropod skull and muscles

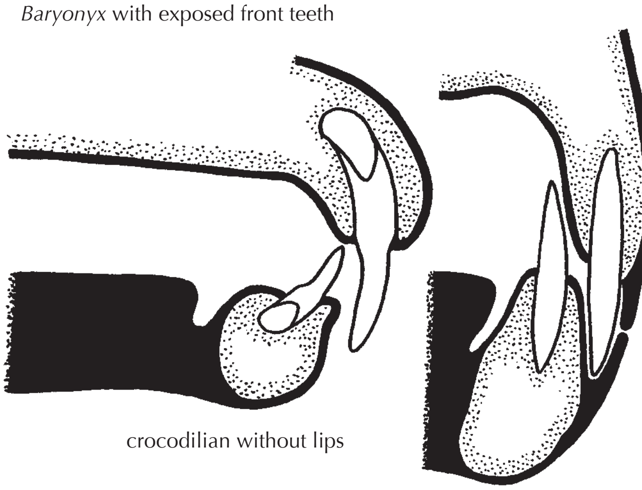


Ornithischian skull and muscles





Baryonyx with exposed front teeth

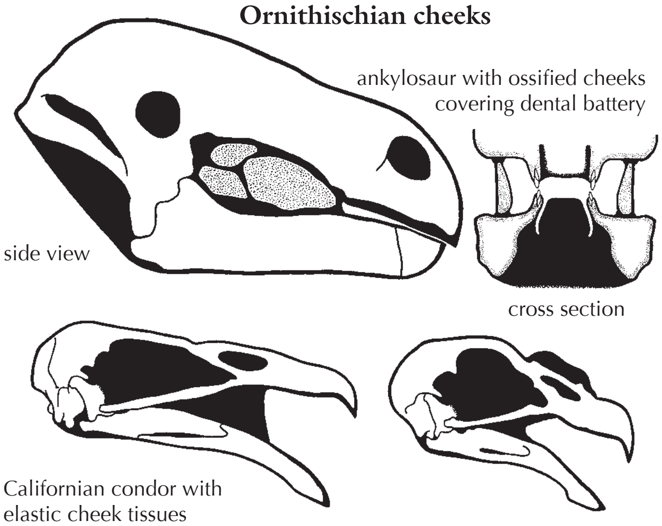


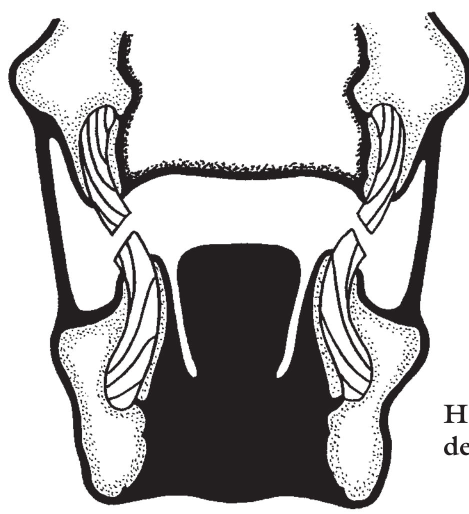
Archosaur lip anatomy

Among amphibians, tuataras, lizards, and snakes, the teeth tend to be set close to one another along fairly sharp-rimmed jaws, and the mouth is sealed and the teeth covered by nonmuscular lips when closed. This arrangement appears to be true of most theropods, and sauropods as well. An exception among theropods would be the spinosaurs, which have a more crocodilian arrangement in which at least the front teeth are widely spaced in separate sockets, so they may have been lipless and their snaggly teeth exposed when the jaws were closed. Some theropods and ornithischians evolved beaks, and it has been suggested that prosauropods had incipient beaks. In ornithischians and therizinosaurs the beak was limited to the front of the mouth, but in some theropods and many birds, the beak displaces all the teeth. Beaked birds lack lips, and most do not have cheeks either. Condors, however, have short mouths because the sides of their jaws are covered by elastic cheek tissues, which differ from the muscular cheeks that cover the side teeth in many mammals. The side teeth of herbivorous prosauropods, the first sauropods, and ornithischians tend to be inset from the side of the mouth; the surrounding spaces are smooth surfaced, and the foramina that feed the soft tissue in the area of the mouth are reduced in number and enlarged in size, indicating that well-developed, probably elastic cheeks covered some or all of the side teeth. Because the chewing dental batteries of many herbivorous dinosaurs were placed very close to one another to maximize the masticatory effect on plant material, cheeks were necessary to keep the bulk of the vegetation from falling out of the sides of the narrow mouth while the vegetation was being chomped down to smaller bits—herbivores with broad mouths that do not chew food do not need such cheeks. Dinosaur cheeks were best developed in ornithischians, to the degree of actually being ossified in some ankylosaurs, in which the cheeks extend all the way to the beak.

Set in sockets, all dinosaur teeth were constantly replaced through life in the manner of reptile teeth. Teeth ranged from blunt, leaf-shaped dentition suitable for crushing plants to serrated blades adapted to piercing flesh. Like the teeth of today's carnivores, those of predatory theropods were never razor sharp, as is often claimed: one can run a finger firmly along the serrations without harm. The teeth of iguanodonts and especially hadrosaurs and ceratopsids were concentrated into compact dental batteries made up of hundreds of teeth, although only a minority formed the plant-processing pavement at a given time. A few sauropods also evolved fast-replacement dental arrays, in their case at the front edge of the jaws where the teeth cropped

Ornithischian cheeks





Hadrosaur dental battery

plant material. Because dinosaurs were not lizards or snakes, they lacked flickering tongues. Dinosaurs had well-developed hyoids, suggesting that the tongues they supported were similarly developed. In predatory theropods the tongue was probably simple and inflexible. The tongues of herbivorous dinosaurs were likely to have been more supple and complex in order to help manipulate and, in the case of ornithischians, chew fodder.

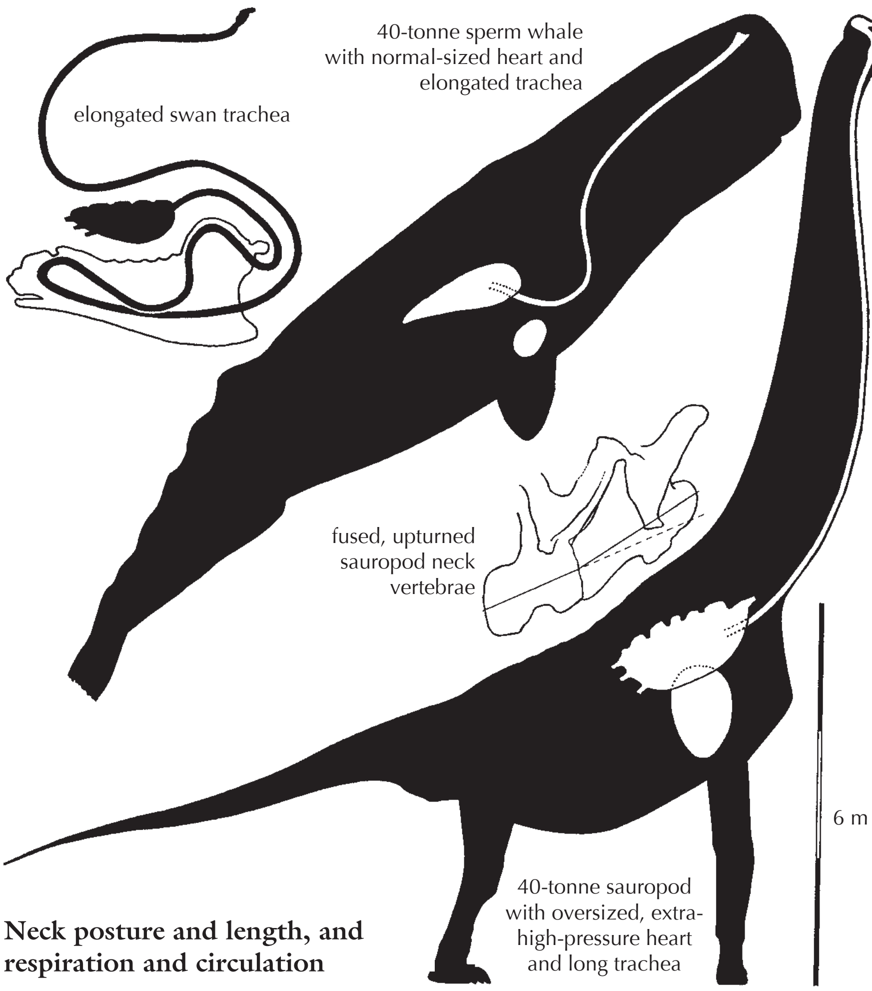
In some large dinosaurs the eyes were in the upper part of the orbit. Bony eye (sclerotic) rings often show the actual size of the eye both in total and indirectly in that the diameter of the inner ring tends to closely match the area of the visible eye when the eyelids are open. Most dinosaurs had large eyes, yet relative eye size decreases as animals get bigger. Although the eyes of giant theropods were very large, they looked small compared to the size of their heads. Even the eyes of ostriches, the biggest among living terrestrial animals, do not appear that large on the living animal. In the predatory daylight raptors, a bony bar running above the eyeball provides the fierce "eagle look." Interestingly, the flesh-eating theropods lacked this bar, but it was present in some of the smaller ornithischians, giving these plant eaters a more intimidating appearance than that of equally peaceful, doe-eyed herbivorous mammals. The purpose of the eye bar is not well understood. It may shade the eyes from glare, it may strengthen the skull during feeding and chewing, and it may have protected the eyes of burrowing ornithopods from dirt and dust. Whether the pupils of dinosaur eyes were circular or slit shaped is not known. The latter are most common in nocturnal animals, and either may have been present in different species. The eyes of birds and reptiles are protected by both lids and a nictitating membrane, so the same was presumably true in dinosaurs.

The outer ear is a deep, small depression between the quadrate and jaw-closing muscles at the back of the head. The eardrum was set in the depression and was connected to the inner ear by a simple stapes rod. The orientation of the semicircular canals of the inner ears is being used to determine the posture of dinosaur heads. For example, short-necked diplodocoid heads pointed straight down according to this method, implying that they grazed ground cover. The situation may, however, be more complicated, reducing the reliability of the method. In living animals the relationship between the orientation of the canals and the normal carriage of the head is not all that uniform. That animals position their heads in different manners depending on what they are doing does not help. Giraffes feed with the head pointing straight down when browsing on low shrubs, or horizontally, or straight up when reaching as high as possible, so the orientation of the semicircular canals is not particularly informative. It is widely thought that the broad-beaked, duck-billed hadrosaurs were grazers, so their heads should often have been held directed straight down. Yet their semicircular canals favor a horizontal head posture. The semicircular canals of at least some prosauropods seem to show that they typically held the nose tilted somewhat upward, an odd pose not normal to large herbivores. It seems that the posture of the semicircular canals is determined as much by the orientation of the braincase with the rest of the skull and does not reflect the orientation of the head as well as has been thought.

The necks of many dinosaurs tend to articulate in a birdlike S curve, as they do in most theropods and ornithopods. The beveling of the vertebrae is especially strong in some theropods. If anything, animals tend to hold their necks more erect than the articulations indicate. In other groups, such as ankylosaurs and ceratopsids, the necks were straighter. There has been a tendency to make dinosaur necks too short by placing the shoulder girdle too far forward. Even ankylosaur necks were long enough to accommodate two or three well-spaced armor rings. The flexibility of dinosaur necks ranged from low—the first few vertebrae of the short-necked ceratopsids were even fused together—to fairly high in longer-necked examples, but no dinosaur had the special adaptations that make bird necks exceptionally mobile.

The posture and function of the long necks of sauropods have become controversial. Some researchers propose a simplistic model in which the necks of all sauropods were held nearly straight and horizontally and, in a number of cases, could not be raised much above shoulder level. This was most true of one group, the short-necked diplodocoids. Otherwise the situation is complex and in many regards is not well understood. Many of the sauropod necks that have been restored in a straight line show obvious misarticulations or are based on vertebrae that are too distorted and incomplete to be reliably articulated. The vertebrae of the necks of different giraffe individuals do not articulate in a consistent manner: they can range from arcing strongly downward to strongly erect. This reflects the differing thickness of the cartilage pads between the vertebrae and demonstrates that the cartilage as well as the bones must be present to articulate necks properly. This is an obvious problem in that cartilage is rarely preserved in fossils. In many dinosaur skeletons the vertebrae are found jammed tightly together, probably because the intervening cartilage disks dried out after death and pulled the bones together.

In some articulated dinosaur skeletons, the vertebrae are still separated by the substantial gap that had been filled by the cartilage. The only example of the cartilage between the vertebrae being preserved in a sauropod neck is in two neck-base vertebrae of an old camarasaur that fused together before death. Contrary to the prediction based on horizontal-necked sauropods, the vertebrae are flexed upward as though the neck was held above shoulder level. Because sauropod necks had so many vertebrae, just 10 degrees of upward flexion between each pair allowed most of the sauropods to raise most of their necks nearly vertically, with the head far above shoulder level. Ostriches and giraffes hold their necks at different angles, and it is possible that sauropods did not really have specific neutral neck postures. There is no reason to assume that sauropods did not hold their necks higher than the bones may seem to indicate, and a growing number of researchers favor the probability that many sauropods held their heads high.



normally fused the way they often are in birds. As in lizards, crocodilians, and birds, the front ribs are strongly swept back in articulated dinosaur skeletons of all types; they are not vertical as they are in many mammals. Dinosaur belly ribs tend to be more vertical, but this condition is variable. The bellies and hips of the flesh-eating theropods were narrow, reflecting the small size of their digestive tracts as well as their athletic form. Big-game-hunting predators gorged after a kill and then fasted until the next one, so their bellies were hollow when they were on the hunt. The same should have been true of flesh-eating theropods, although abdominal air sacs, if present, may have filled out some the space of the gut even when the animals were hungry. The abdomens and hips of herbivorous dinosaurs were broader in order to accommodate more capacious digestive tracts.

Some plant-eating dinosaurs, therizinosaur theropods, titanosauriform sauropods, pachycephalosaurs, most stegosaurs, and especially ankylosaurs took the broadening of the belly and hips to an extreme, to a degree that seems absurd in the fattest of the armored dinosaurs. The shoulder blades of ankylosaurs were even twisted along their long axis to fit onto the rapid shift from the narrow shoulders to the fat abdomen. Because dinosaur trunk vertebrae and ribs formed a short, fairly rigid body with the shoulder and hip girdles close together, the trunk musculature was rather light, like that of birds. Theropods and prosauropods retained gastralia, a series of flexible bony rods in the skin of the belly. Each segment of the gastralia was made of multiple pieces. This may have been necessary in prosauropods because they flexed their trunks while running on all fours. Theropods needed flexible gastralia because their bellies changed dramatically in size as they gorged and fasted between hunts. In therizinosaurs the gastralia became more rigid, probably because these rigid-trunked herbivores always kept their abdomens full of fermenting fodder. These structures were absent in sauropods and ornithischians.

The tails of dinosaurs were highly flexible in most stegosaurs, theropods, and sauropodomorphs, especially the titanosaur sauropods, whose ball-and-socket joints may have allowed the tail to be arced directly over the back. In the sickle-clawed dromaeosaurid theropods, club-tailed ankylosaurids, and ornithopods, part or all of the tail was stiffened by ossified tendons, with the tails of iguanodonts and hadrosaurs being especially inflexible.

Neck posture and length, and respiration and circulation

Giraffe necks are not heavily muscled despite their having solid vertebrae that had to support a large head. Sauropod necks held up much smaller heads and were highly pneumatic, so they should not have been heavily muscled either. In some sauropods tall shoulder spines indicate that a fairly deep set of nuchal tendons helped to support the neck. In a number of other sauropods the neural spines were doubled in order to improve neck support. The upper neck muscles of big-headed pachycephalosaurs and ceratopsians should have been powerfully built, and some ceratopsids had the tall shoulder withers that indicate the presence of deep nuchal tendons. Mummies show that the hadrosaurs, whose neck vertebrae appear slender relative to their rather large heads, had deep nuchal tendons to help hold them up. The predatory theropods probably had the strongest neck muscles, which helped drive the teeth deeper into the flesh of their prey.

The trunk vertebrae of dinosaurs articulated either in a straight line or, more often, in a dorsally convex arch that varied from subtle to very strong. The nature of the vertebral articulations, and in many cases ossified interspinal tendons, indicates that dinosaurs had stiffer backs than lizards, crocs, and most mammals, although the trunk vertebrae of dinosaurs were not

In most dinosaurs the hip vertebrae and tail were in much the same line as the trunk vertebrae. Because tail drag marks are very rare among the immense number of trackways known for all the major dinosaur groups, the old-style convention of persistently tail-dragging dinosaurs cannot be correct. This is true even in those dinosaurs whose tail base was swept downward. In therizinosaurs and some sauropods the hips and tail were flexed upward relative to the trunk vertebrae. This allowed the trunk to be held strongly pitched up while the hips and tail remained horizontal, increasing the vertical reach of the head while the dinosaur retained the ability to move on the hind legs. Because all dinosaurs bore most of their weight on their hind legs and usually had long tails that acted as counterweights to the body, all of them could rear up, even the few that had arms that were longer than their legs.

Unlike many mammals, no dinosaur had hands that looked like its feet. The hands always lacked a heavy central pad, even in the giant quadrupeds. Sauropods, stegosaurs, iguanodonts, and hadrosaurs united their short fingers into a hoof-like hand by encasing them in single, tight pad. A very distinctive character of theropods, prosauropods, some sauropods, and some ornithischians was the big-clawed, inwardly directed thumb weapon, which could be held clear of the ground when walking with the arms. The palms of dinosaurs always faced partly or strongly inward, especially in bipedal examples. In some of the larger dinosaurs—iguanodonts and hadrosaurs, armored dinosaurs, ceratopsids, and sauropods—the hind feet were underlain by a large central pad similar to those of rhinos and elephants.

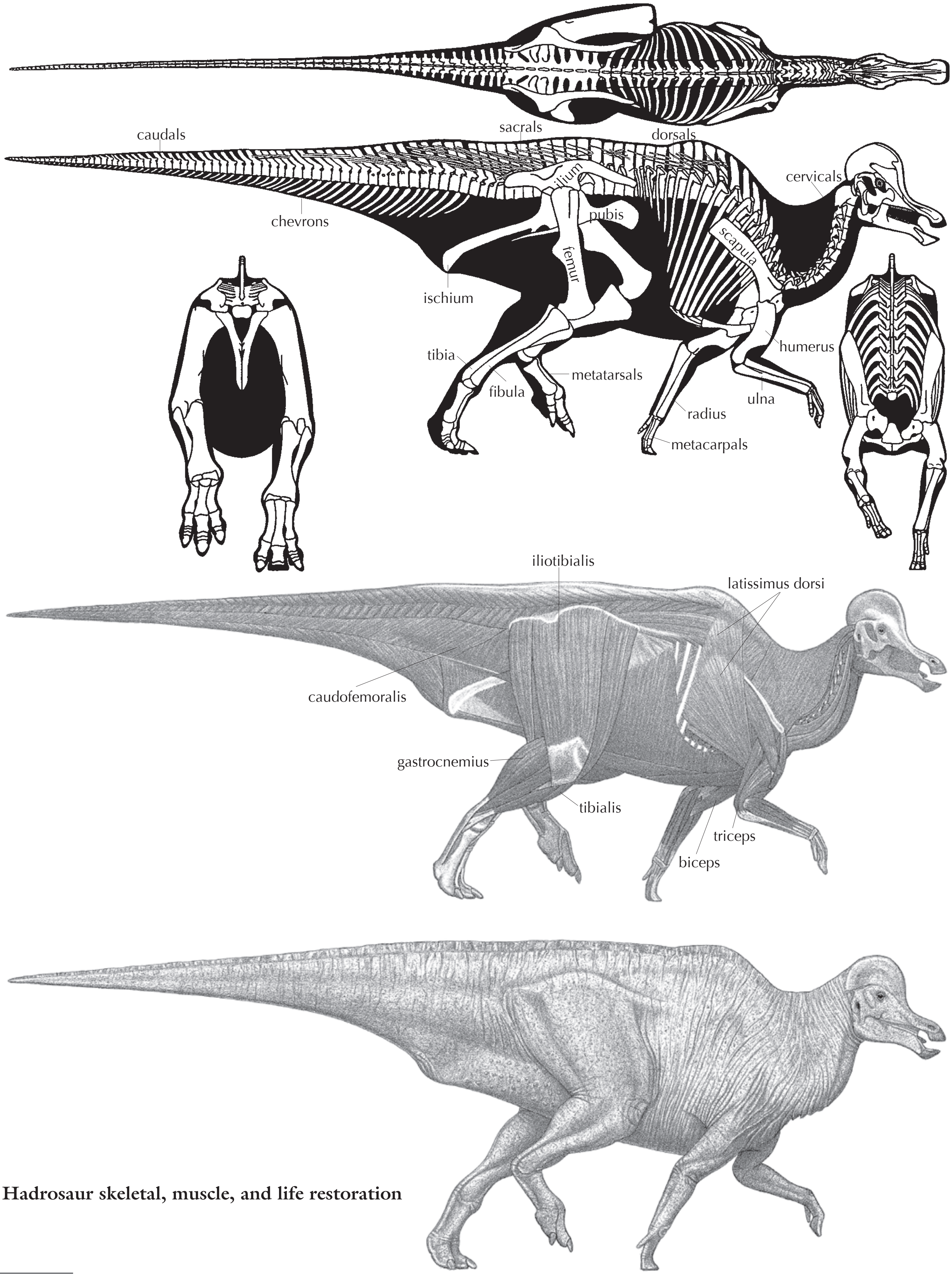
The front of the rib cage of dinosaurs was narrow from side to side in order to accommodate the shoulder girdle, both sides of which nearly met one another on the chest, and the shoulder joint was immediately in front of the rib cage. This differs from mammals, in which the shoulder joint is on the side of the chest. In theropods, including birds, the shoulder girdle is fixed in place, partly by a fused furcula that braces both scapula blades. Many reptiles and mammals have mobile shoulder girdles that help increase the stride length of the arms. This appears to have been true of quadrupedal dinosaurs because their clavicles are not fused together, or they do not contact one another, or they are lost. In side view, the scapula blade of most dinosaurs was subvertical as in most tetrapods, not horizontal. The exceptions are the most birdlike theropods and birds themselves, whose scapula blades are horizontal.

In flying birds the shoulder joint faces sideways and upward so the arms can be held out to the side and raised vertically for flapping. In many predatory theropods the arms could also be swung laterally to grapple with prey. But even in winged protobirds like *Archaeopteryx* the arms could not be directed straight up. When dinosaurs were walking or running, trackways show that neither their arms nor legs were sprawled sideways like those of lizards. It is difficult to restore the precise posture of dinosaur limbs because in life the joints were formed by thick cartilage pads similar to those found on store-bought chickens, which are immature. Even so, some basics can be determined. The shoulder joints of quadrupedal dinosaurs faced down and backward so that the arm could swing below the shoulder joints, and the cylindrical hip joints forced the legs to work below the hips. But this does not mean that the erect limbs worked in simple, entirely vertical fore-and-aft planes. The elbows and knees, for instance, were bowed somewhat outward to clear the body, a feature common to many mammals as well. Trackways show that unlike the hands of mammals, which are often near the body midline when walking, the hands of dinosaurs were almost always separated by at least two hand widths, the hands were rarely placed closer to the midline than the feet, and the hands were often farther from the midline than the feet. This was because the arms were oriented so that the hands were either directly beneath the shoulder joints or a little farther apart. The hind feet of dinosaurs often did fall on the midline, even among some of the largest quadrupeds, and were never separated by much more than the width of a single hind print, even among the broadest-hipped sauropods and armored dinosaurs.

Dinosaur hands and feet were digitigrade, with the wrists and ankles held clear of the ground. Most dinosaurs retained the strongly flexed shoulder, elbow, hip, knee, and ankle joints that provided the springlike limb action needed to achieve a full run in which all feet were off the ground at some point in each complete step cycle. In addition, the ankle remained highly flexible, allowing the long foot to push the dinosaur into the ballistic stride. This was true of even the most gigantic theropods, ornithopods, ankylosaurs, and ceratopsids, which reached 5 to 15 tonnes. The knee joints of flexed-limbed dinosaurs were not fully articulated if they were straightened. Humans have vertical legs with straight knees because our vertical bodies place the center of gravity in line with the hip socket. In bipedal dinosaurs, because the head and body were held horizontally and were well forward of the hips, the center of gravity was ahead of the hip socket even with the long tail acting as a counterbalance, so the femur had to slope strongly forward to place the feet beneath the center of gravity. This arrangement is taken to an extreme in short-tailed birds, whose femur is nearly horizontal when they are walking in order to place the knees and feet far enough forward; in running, the femur of birds swings more strongly backward.

That dinosaurs normally retained thick cartilage pads in their limb joints throughout their entire lives, no matter how fast or big they became, is a poorly understood difference between them and birds and mammals that have well-ossified limb joints. The manner in which dinosaurs grew up and matured may explain the divergence. In terms of locomotory performance it does not seem to have done dinosaurs any harm and may have had advantages in distributing weight and stress loads.

Two groups of dinosaurs, the stegosaurs and sauropods, evolved elephantine, more columnar, straighter-jointed limbs. The configuration of the knee was altered so that it remained fully articulated when straight. In addition, the ankle was less mobile, and the hind feet were very short. This suite of



Hadrosaur skeletal, muscle, and life restoration

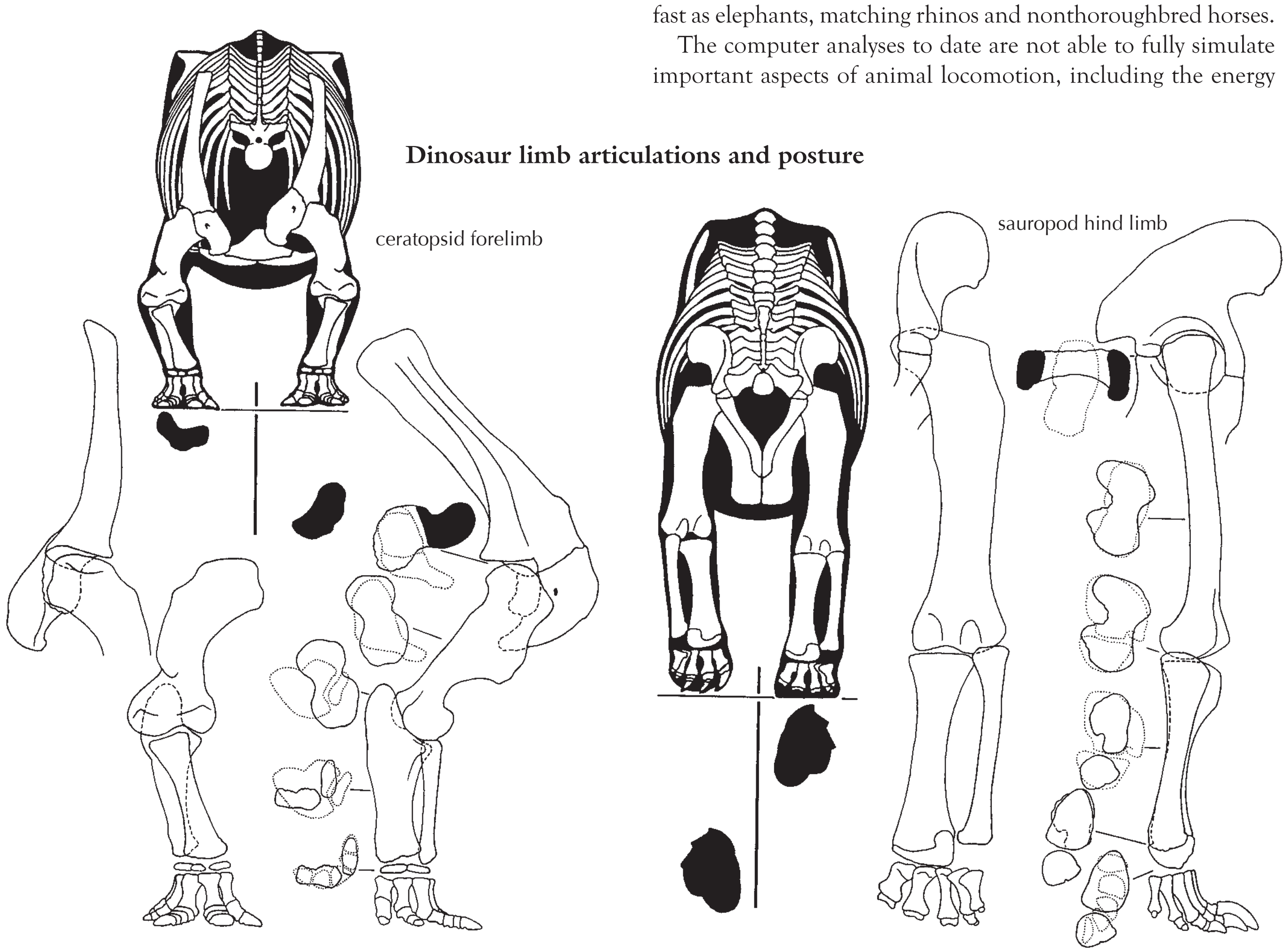
Dinosaur trackways, drawn to same stride length

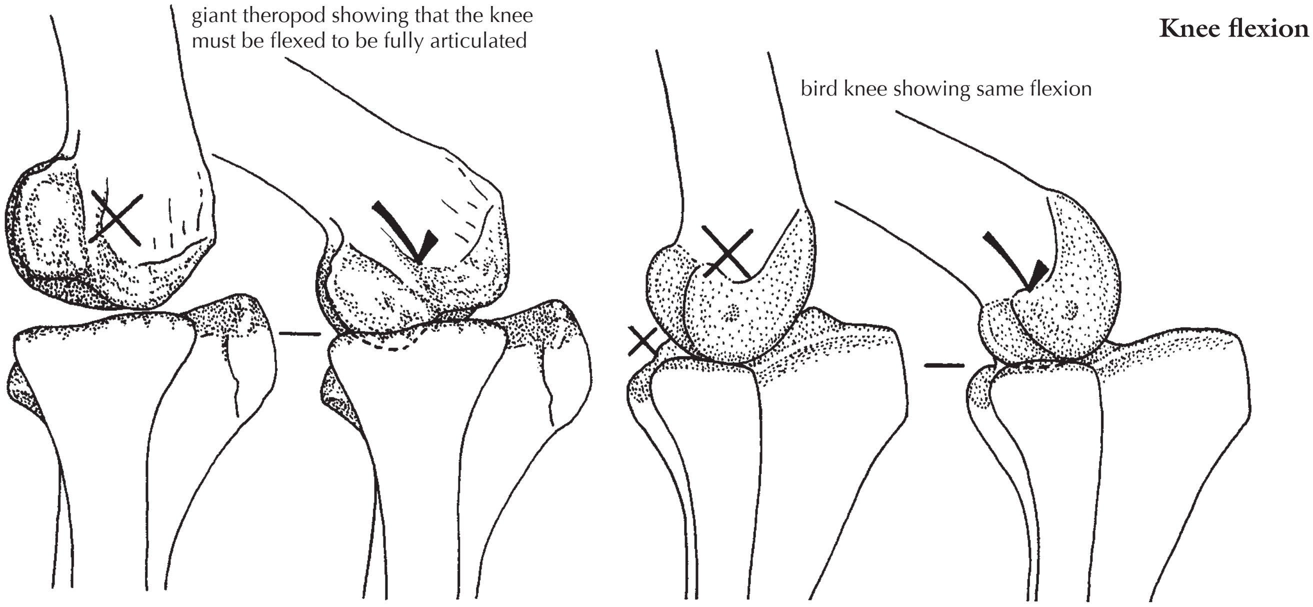
adaptations prevents the body from being propelled into a true run regardless of size: juvenile elephants cannot move any faster than their parents. Instead, at least one foot remains in contact with the ground at the highest speed.

The straight-limbed dinosaurs should not have been able to move faster than elephants, which cannot exceed 25 km/h (15 mph). Nor is it a problem to conclude that small and medium-sized dinosaurs with long, slender, flexed legs were able to run at speeds comparable to those of similar-sized ground birds and galloping mammals, which can reach 40–60 km/h (25–40 mph). Difficulties arise when trying to estimate the top speeds of flexed-limbed dinosaurs weighing many tonnes. Computer analysis has calculated that *Tyrannosaurus* could reach a top speed ranging from no better than that of a similar-sized elephant up to 40 km/h, the speed of a sprinting human. Because big-hipped, birdlike *Tyrannosaurus* was much better adapted for running than are elephants, it is unlikely that it was similarly slow, and other estimates suggest that giant theropods could run almost twice as fast as elephants, matching rhinos and nonthoroughbred horses.

The computer analyses to date are not able to fully simulate important aspects of animal locomotion, including the energy

Dinosaur limb articulations and posture





storage of prestretched elastic leg tendons and the resonant springlike effect of the torso and tail. Nor has the ability of these programs to successfully calculate the performance of extreme animals been better established by showing how the most extreme of all dinosaurs, the supersauropods, managed to even stand upright much less move their whale-sized bodies. This important yet unanswered question is all the more pressing because trackways prove that the greatest sauropods walked without the support of water, yet they appear no better proportioned to support their mass than are the slow-moving elephants, which are ten or more times smaller. Did the supersauropods not need "super" adaptations beyond those seen in elephants to move about the Mesozoic landscapes, or did special adaptations such as stronger muscle fibers and pretensed tendons evolve to solve the problem? If the latter proves true, then other giant running dinosaurs may have used special adaptations to move faster than our computer models are indicating.

An important aspect of assessing dinosaur speed and power is the mass of the limb muscles, which tend to make up a larger percentage of the total mass in fast runners than in slower animals. Because the muscles are not preserved in dinosaur fossils, it is not possible to accurately restore the speed of a given dinosaur—at best it can only be approximated. The complex limb muscles of living mammals are the heritage of the unusual history of the early members of the group. Dinosaurs retained the simpler muscle patterns of reptiles, which are still seen in birds. A major muscle present in many reptiles and most dinosaurs, but not in birds and mammals, was the tail-based caudofemoralis, which helped pull the hind limb back during the propulsive stroke.

Although the absolute size of dinosaur muscles cannot be exactly determined, their relative size between the different groups can be approximated. In reptile hips the ilium is so short that the thigh muscles have to be narrow, limiting their size. The much longer ilia of birds and mammals anchor a broad and powerful set of thigh muscles. The ilium of the early herrerasaurs and prosauropods was short, so they must have had narrow thigh muscles. In other dinosaurs the ilium was longer and deeper, anchoring a larger set of thigh muscles able to produce more sustainable power. This trend was taken to an extreme in some dinosaurs. In the ostrichlike ornithomimids and tyrannosaurids, the oversized pelvis indicates the presence of exceptionally large leg muscles able to power high speeds. The ceratopsid dinosaurs had even longer hips, which probably supported the big leg muscles required to propel the fast charges needed to fend off the similarly strong-muscled tyrannosaurs. It is interesting that the enormous sauropods did not have especially large ilia. That is because they did not need large muscles to move at a fast pace. The same is true of elephants, which also lack large muscles below the knees because the feet that the shank muscles help operate are very short and nearly immobile. A similar situation was true of sauropods and stegosaurs. Faster animals have a large bundle of shank muscles that operate the long, mobile foot via long tendons. In bipedal dinosaurs, including birds, the large, drumstick-shaped collection of muscles below the knee is anchored on the cnemial crest projecting forward of the knee joint.

Fossil burrows indicate that some small dinosaurs dug burrows. This explains why small, bipedal ornithischians often had oversized shoulder girdles—they anchored the powerful upper arm muscles needed for digging with their broad hands.

Restorations of dinosaurs commonly simplify their surface contours, making their necks, tails, and legs into rather simple tubes and smoothing over the topography of the body. In sauropods the bulge of each neck vertebra was probably visible on the side of the neck, as it is in giraffes. Because the trachea and esophagus of sauropods were probably tucked up between their

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