

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 bird-like *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 the best hunting grounds 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*, *Apatosaurus*, *Diplodocus*, and *Camarasaurus*, which really were elephantine quadrupeds, the proto-iguanodont *Camptosaurus*, and 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 duckbilled *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* (= *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 actually had laid and incubated them. As it happened, the Mongolian expeditions were somewhat misdirected. Had paleontologists also headed northeast of Peking, 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 to head northeast contributed to a set of problems that seriously damaged

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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 been 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 art 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 brought seemingly 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, involve climactic scenes in which sauropod skeletons at a semifiictional New York museum collapse 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 attention.

Despite the problems, discoveries continued. In an achievement remarkable for a nation ravaged by the Great Patriotic War and 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 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 ostrich-like 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 descendents 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 descendents 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 over 6-mile-diameter asteroid 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 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 golden age of dinosaur discovery and research, which is surpassing that which has gone on 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 have portrayed dinosaurs with the “new look” that lifted tails in the air and got the feet off the ground to represent the more dynamic gaits that were in line with the more active lifestyles the researchers now favored. This artist and researcher 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.

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 see 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 protodinosaur, finally showing that the very beginnings of dinosaurs started among surprisingly



The dinobird *Deinonychus*

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*, and the oversized theropods such as *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 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 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 theropod *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. Further 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

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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 bristle protofeathers. It has just been realized that it is 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 versus science. The feathered dinosaurs soon included the potentially oviraptorosaur *Caudipteryx*, the tail fan of which may be one of only two cases in which part of a dinosaur's color pattern is preserved. 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 that dromaeosaurs not only first evolved as fliers but that they were adapted to fly in manner quite different from the avian norm. The therizinosaur *Beipiaosaurus* has a wild array of display feathers that contribute to its looking 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 bristle 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.

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 this researcher and artist was young, he 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 descendents was beyond

The flying dinosaur
Sinornithosaurus
attacking *Psittacosaurus*



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 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 ancient muds. Dinosaurs are no longer so mysterious. Even so, the research is nowhere near its end. To date over six hundred valid dinosaur species in about four 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 unearthed. Reams of work based on as-yet-undeveloped technologies and techniques are required to further detail both dinosaur biology and the world they lived in. 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 tuaturas, true lizards and snakes, crocodylians, and birds. The Archosauria is the largest and most successful group of diapsids and includes crocodylians 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 included the ancestors of crocodylians 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 descendents. 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.

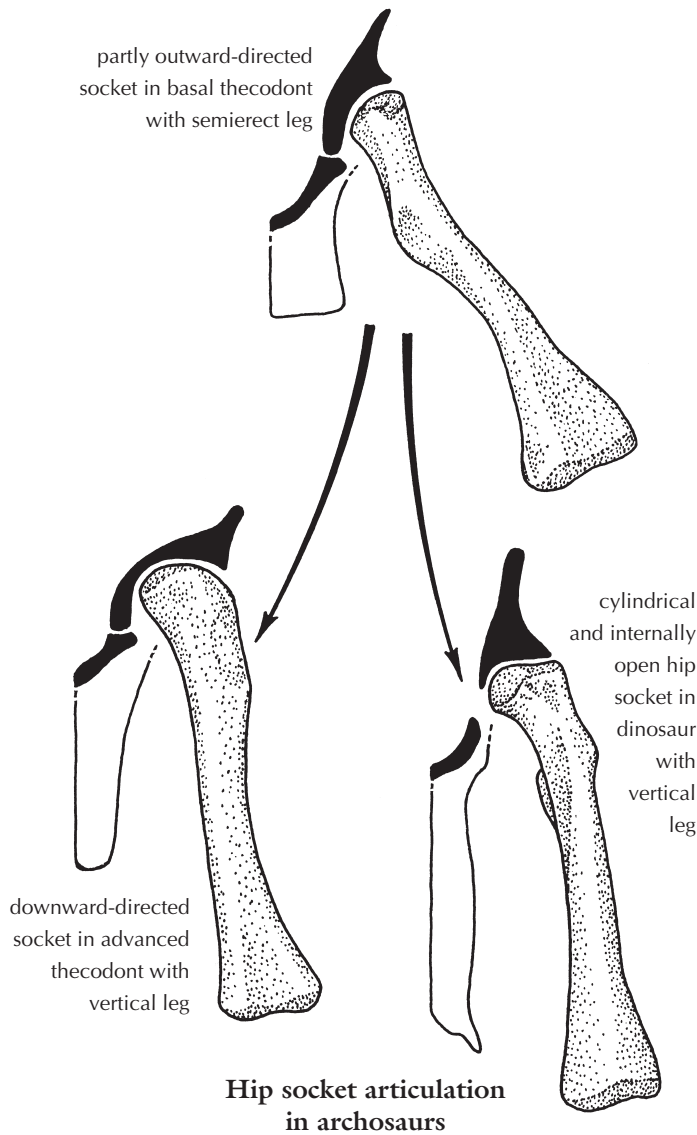
In anatomical terms one of the features that most distinguishes dinosaurs centers on the hip socket. The head of the femur is a cylinder turned in at a right angle to the shaft of the femur that fits into a cylindrical, internally open hip socket. This allows the legs to operate in the nearly vertical 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 “hindlimb 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 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

**A basal archosaur,
*Euparkeria***



DATING DINOSAURS



from nearly bird-like types such as the sickle-clawed dromaeosaurs to 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 as per 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, 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, whereas 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 about 220 million years ago and then disappearing at the end of the Cretaceous 65.4 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 distinctive stratigraphic beds that are called formations. For example, *Apatosaurus*, *Diplodocus*, *Barosaurus*, *Stegosaurus*, *Camptosaurus*, *Allosaurus*, and *Ornitholestes* are found in the Morrison Formation of Western North America that was laid down in the Late Jurassic, from 156 to 148 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

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by the Cenozoic—that contained the three progressively younger periods, 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 only works on bones and other specimens going back 50,000 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 an 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 ash falls similar to the one deposited by Mount St. Helens over neighboring states that leave a distinct layer in the sediments. Assume that one ash fall 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 it is known 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 Mesozoic–Cenozoic boundary that marks the extinction of dinosaurs, for example, is now dated to 65.4 million years ago, with a plus or minus error of only 100,000 years, a total error of just a third

of a percent. Attempts are under way to pin down the date that the extraterrestrial impact that ended the dinosaur era to within 10,000 years. 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 includes some marine deposits laid down at the same time near its edge. The marine sediments contain some small organisms that only lasted for a few million years in time. Somewhere else in the world the same species of marine life was deposited in a marine formation that include volcanic ash falls that have been radiometrically dated to 84 to 81 million years. It can then be concluded that the dinosaur in the first formation is also 84 to 81 million years in age.

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, because they lack the needed age determinants, and/or because they have not been sufficiently well examined, that 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 short life spans. 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 the 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

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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 per 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 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-crocodylian 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.

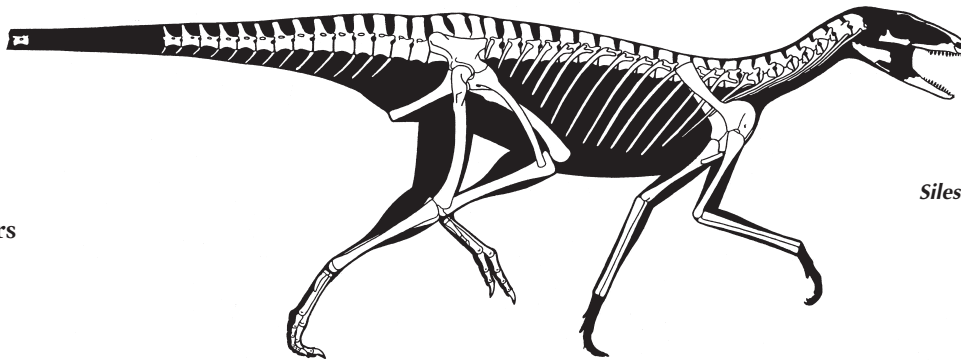
At the beginning of the first period of the Mesozoic, the Triassic, the global fauna was severely denuded. As it recovered, the few remaining therapsids enjoyed a second evolutionary radiation and again became an important part of the wildlife. This time they had competition as the archosaurs also underwent 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 become inturned; 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. Also coming onto the scene were the crocodylians, the only group surviving today that reminds us what the archosaurs of the Triassic were like. Triassic crocodylians 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. Crocodylians, like many of the thecodonts, had a very un-dinosaurian 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; not yet known is whether other nondinosaurian archosaurs were also covered with thermal fibers.

In the Landian, the last stage of the Middle Triassic, quite small predatory archosaurs appeared exhibiting 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. These lagosuchian protodinosaurians are at first known only from South America. Whether this means the group originated there or if they were more widespread is not known. Protodinosaurians would survive only until the Norian, by which time they had spread at least to North America. Protodinosaurians show that dinosaurs started out as little creatures.

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 early Norian stage, perhaps because these early dinosaurs did not have the aerobic capacity to compete with their new competitors. The Norian saw the appearance of the great group that is still with us, the bird-footed avian-type theropods, whose large hips and beginnings of the avian-type respiratory system imply an 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 quadripedal 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 protodinosaurians, 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

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*Lagosuchus**Silesaurus***Protodinosaur**

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, there was a tendency for faunas 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 CO₂ 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. 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 are 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 grass and shrublands of today. Tree ferns were common in wetter areas. Even more abundant were the fern- or palm-like cycadeoids, similar to the cycads that still inhabit the tropics. Taller trees included water-loving ginkoids, 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; these 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, crocodylians, pterosaurs, and especially dinosaurs

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The Late Triassic *Coelophysis*

sailed through the crisis into the Early Jurassic with little disruption. Apepod 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 crocodylians; there simply were no competitors above a few kilograms in weight. Such extreme superiority was unique in earth history. The Jurassic and Cretaceous were the Age of Dinosaurs.

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 bird-like 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 were the small, chisel toothed, semi-bipedal heterodontosaurs, which establishes that fiber coverings had evolved in some small dinosaurs by this time if not earlier. On the continents, crocodylians 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. Further 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 oceans' floors to lift up, spilling the oceans onto the continents in the forms 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

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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 tetranuran, 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.

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,

mamenchisaurus, dicraeosaurus, 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 semipedal ceratopsians.

The still-small ancestors of tyrannosaurs seem to have been developing at this time, and assorted gracile maniraptor coelurosaurs were numerous. The odd *Scansoriopteryx* with its aye-aye-like finger indicates that some theropods were well-developed climbers. 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 bird-like and probably partly arboreal avepektorans



The Late Jurassic *Giraffatitan* and *Dicraeosaurus*

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that was a major event. The Chinese deinonychosaur *Archiornis* is the earliest dinosaur known to have had large feathers on its arms as well as legs. 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 abilities. A few million years later, when Europe was still a nearshore extension of northeastern North America, the first “bird,” the deinonychosaur *Archaeopteryx*, was extant. Preserved in lagoonal deposits on the northwest edge of the then great Tethys Ocean, its combination of very large arms and long, asymmetrical wing feathers indicate it was part of the process of developing the early stages of powered flight. The advent of the little avepektorans also heralded the first major increase in dinosaurian mental powers as brain size and complexity raised to the lower avian level. Pterosaurs, which retained smaller brains, remained small, and most still had long tails. Although some crocodylians were still small runners, the kind of highly amphibious crocodylians 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, CO₂ 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. Contrary to common impression, the classic umbrella-shaped monkey-puzzle type of araucarian conifer found in modern South America was not a source of food for Jurassic sauropods. Wetter areas were dominated by conifers similar to cypress. Sauropods 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 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 CO₂ levels gradually edged downward, although never down to the modern 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 winter conditions frigid enough to form permafrost. General global conditions were a little wetter than earlier in the Mesozoic, but seasonal aridity remained the rule in most places, and true rain forests continued to be at best scarce.

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 brachiosaur, and especially the broad-bellied titanosaurs predominated.

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 the 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 of Asia with little change in form. Among ceratopsians the small Asian chisel-toothed psittacosaur proliferated, and their relatives, the big-headed protoceratopsids, appeared in the same region. So did the first of the domeheaded pachycephalosaurs. Stegosaur, however, soon departed the scene, the final major dinosaur group to become totally extinct since the prosauropods. This fact 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 ankylosaur became a major portion of the global fauna, their plates and spikes providing protection from the big Laurasian allosauroids and snub-nosed, short-armed abelisaur 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, even though they show no special adaptations for swimming. 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 titanic, tyrannosaurs with similarly long running legs and reduced arms. But the focus of events was among the nearly avian avepektorans. 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 hindlegs. 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 appeared during this period.

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. None were especially large. Among these early birds were the beaked omnivoropterygids, which bear a striking resemblance to the caudipterygid and protoarchaeopterygid

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oviraptorosaurs from the same formation. It is possible that the short-tailed oviraptorosaurs were another group of secondarily flightless dinosaur-birds, ones more advanced than the archaeopterygians and dromaeosaurs. Also appearing by the Early Cretaceous are the herbivorous theropods, the enigmatic, pot-bellied therizinosaurs.

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 crocodylians, making them an increasing threat for dinosaurs coming to water to drink or for other purposes. Some large crocodylians were semiterrestrial and able to attack big dinosaurs on land as well as in the water. Still scampering about were a few small running crocodylians. 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. In the late Early Cretaceous, flowering plants evolved. 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 growing new plants. Also appearing about this time were South American conifers with monkey puzzle foliage.

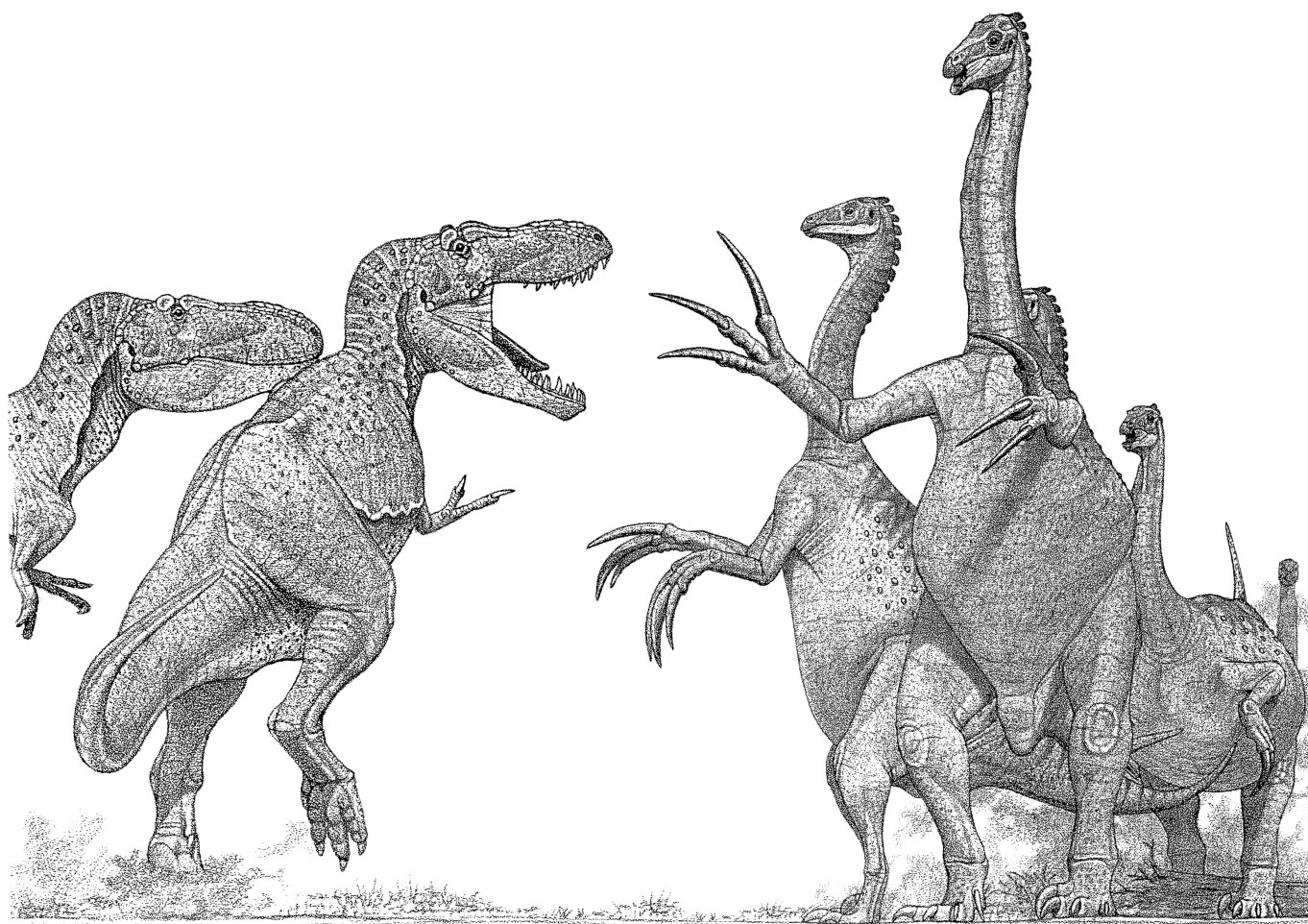
In the Late Cretaceous, which began 100 million years ago, the continental breakup was well under way, with interior seaways often covering vast tracts of land. As CO₂ levels continued to drop, the dark arctic winters became cold enough to match the conditions seen in today's high northern forests, and 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 azhdarchids sported wings of 11 meters (over 35 feet) and outweighed ostriches. Small running crocodylians remained extant, and a few even became herbivorous. As for the conventional freshwater crocodylians, in some locales they become colossi up to 12 meters 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 supercroc 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 high 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 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 and to settle disputes within the species. The iguanodonts faded from the scene in lieu of their descendents, 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 evolved some of the most spectacular dinosaurs, 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 area, largely limited to the modest-sized stretch of North America that lay west of the interior seaway.

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 avepektorans, the deep-headed omnivorous oviraptorosaurs, many exhibiting dramatic head crests, and the small-headed, big-clawed herbivorous therizinosaurs. In both groups some species became quite large. The long- and slender-legged ornithomimids became perhaps the fastest of all dinosaurs, although they were closely matched by the colonial insect-eating Alvarezsaurus.

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The Late Cretaceous *Tyrannosaurus* and *Therizinosaurus*

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. 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 *T. rex*, *Triceratops*, *Torosaurus*, *Ankylosaurus*, *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 fire-

power 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. 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 something went catastrophically wrong.