

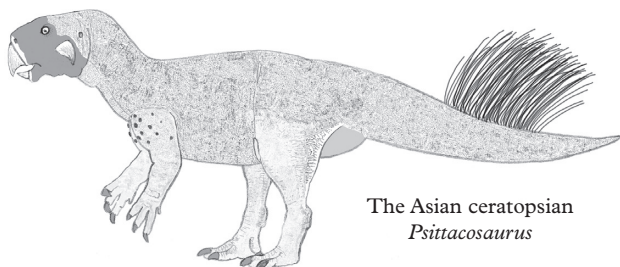
preserving large scales on its feet and the impressions of massive, bulbous toe pads.

See also Allosauroids; Megaraptorans.

Ceratopsians

The Jurassic and Cretaceous ornithischian clade (properly Ceratopsia and often called horned dinosaurs) that includes *Triceratops* and its kin. Ceratopsians are famously (albeit not universally) equipped with a bony frill at the back of the skull, and horns on the nose and above the eyes. *Triceratops* and its relatives—the most familiar of ceratopsians—are united within Ceratopsidae, a mostly North American clade whose species are rhino-like or elephant-like in size. Several other ceratopsian clades are less anatomically remarkable. These demonstrate the main evolutionary trend across the clade: they changed from small, bipedal forms to mid-sized and ultimately gigantic quadrupeds with large, frill-bearing, ornate skulls equipped with enlarged beaks and tooth batteries incorporating complex teeth.

The oldest and least anatomically modified ceratopsians include the chaoyangsaurids of Late Jurassic China (and perhaps Early Cretaceous Germany) and the psittacosaurids of Early Cretaceous eastern Asia. The members of these clades are 1–2 m (3–6.5 ft) long and bipedal. They didn't have frills or horns, but their skulls are broad across the cheeks and equipped with a narrow, hooked beak where an extra bone—the rostral—helped enlarge and provide mechanical support for the beak in the upper jaw. The best known archaic ceratopsian is *Psittacosaurus*, a dinosaur known from hundreds



The Asian ceratopsian
Psittacosaurus

of specimens that belong to more than 10 species. These come from sediments deposited over a period of around 20 million years, an atypically long time for a dinosaur taxon typically regarded as a genus.

Around 135 million years ago, psittacosaur-like ceratopsians gave rise to the clade Neoceratopsia. Early neoceratopsians—initially similar to psittacosaurus in size and shape—differed in having a short bony frill and a shallow snout. By around 110 million years ago, they had diversified and given rise to several additional clades, some of which evolved quadrupedality and large size. The leptoceratopsids—a mostly quadrupedal clade of Asia, North America and Europe—persisted to the end of the Cretaceous. Rather better known are the coronosaurians, archaic members of which include *Protoceratops* of eastern Asia. *Protoceratops*-like coronosaurians gave rise to mid-sized (as in, about 3.5 m [11.5 ft] long) quadrupedal forms like *Zuniceratops* from the southern US, the first ceratopsian to possess supra-orbital horns. And *Zuniceratops*, in turn, appears close to the ancestry of the ceratopsids. There's enough to say about ceratopsids that they get their own section.

Most of ceratopsian evolution happened in Asia, but the clade appears to have moved in and out of North America during its history. If *Zuniceratops* really is close to ceratopsid ancestry, it might be that ceratopsids originated in North America. But another near-ceratopsid—*Turanoceratops*—is from Uzbekistan, so it's difficult to say. Did ceratopsians occur elsewhere? Suggestions that fragmentary fossils from South America and Australia might be ceratopsians have been made but can't be verified.

Tracks and the sediments in which their remains are found show that ceratopsians were terrestrial animals of forested places, though some (like *Protoceratops*) inhabited deserts. It's been suggested that some ceratopsians might have been amphibious, either because they're vaguely hippo-shaped, because their remains have been preserved in aquatic environments, or because the tall bony tail spines of certain species might have supported a fin. These claims rely on the picking of one or two bits of evidence and the ignoring of others. It isn't beyond possibility that some ceratopsians were animals of watery habits but more study is needed before we can accept these ideas.

The wide, bulky bodies, shearing beaks and tooth batteries of ceratopsians show that they were herbivores of high-fiber plants, and they likely fed on plants that grew within 1–2 m (3–6.5 ft) of the ground. A fun idea which has enjoyed a bit of traction in the paleoart community is that ceratopsians might, on occasion, have exploited carcasses and chewed on bones, and it's possible that the smaller species were omnivorous. The narrow beaks, powerful jaws, and fierce appearance of these

dinosaurs makes it possible that they were formidable and aggressive, and able to put up a good fight should a predator fail to get the upper hand right away. This is, of course, wholly speculative; good luck demonstrating it scientifically.

One of the world's most remarkable fossils—dubbed the fighting dinosaurs and discovered in Mongolia in 1971—preserves a *Protoceratops* and *Velociraptor* locked in combat. Both seem to have died after being buried by sand. The *Velociraptor*'s left hand is hooked over the *Protoceratops*' face while its left foot is wedged against the ceratopsian's neck. But the *Protoceratops* has the *Velociraptor*'s right arm in its mouth and is in a crouching pose over the *Velociraptor*, so it isn't obvious that the *Velociraptor* has the upper hand, no pun intended.

Experts have disagreed on the speed and agility of these animals. All ceratopsians smaller than sheep were likely swift runners, but this is less clear for the big ones. Bakker argued in his writings of the 1970s and 80s that *Triceratops* had the bone strength, muscle and tendon size, proportions, and degree of limb movement to allow galloping, and his 1971 illustration of a galloping *Chasmosaurus* pair is an iconic image of the Dinosaur Renaissance. More recent efforts to test these claims have found that a fast run or trot was possible, but that galloping à la Bakker is not likely.

Finally, what about the function of those frills and horns? These massive, flamboyant structures surely evolved primarily as signaling structures or for use in combat, perhaps during the mating season. They might *also* have had roles in predator defense, heat-dumping, tree-breaking, or whatever, but their evolution was

driven mostly by the pressures of sexual selection, just as with antlers, antelope horns, peacock tails, and chameleon casques. Scars, pits, and broken horn tips confirm that ceratopsids fought with their horns and frills.

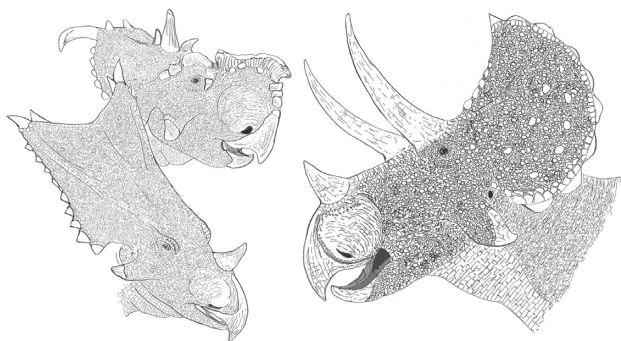
A particularly excellent book that reviews our knowledge of ceratopsians and the history of research on them is Peter Dodson's 1996 *The Horned Dinosaurs*.

See also Ceratopsids; Marginocephalians.

Ceratopsids

The largest, most diverse ceratopsian clade, and the one that includes the big, long-frilled, long-horned taxa like *Styracosaurus*, *Chasmosaurus*, and *Triceratops*. *Triceratops* and a few related kinds were truly gigantic, in cases reaching 9 m, 10 tonnes (29.5 ft, 11 tons), and with skulls more than 2.5 m (8 ft) long. Ceratopsids are almost entirely North American, with one exception, discussed below. Ceratopsid frills are fantastically variable, differing in size and shape and also in the form, number, and position of projections around their edges, and along the midline and apex.

Ceratopsids underwent major diversification in North America, their most notable evolutionary event being the split into the short-frilled, short-faced Centrosaurinae and long-frilled, long-faced Chasmosaurinae at around 80 million years ago. Centrosaurines generally lack horns over the eyes (termed supraorbital horns), while chasmosaurines generally have long ones. The existence of these two clades was recognized by the early 1900s, but *Triceratops*—one of the first ceratopsids to be discovered and named—was always controversial, since it has a short frill like a centrosaurine but a long



Left to right: *Chasmosaurus*, *Pachyrhinosaurus*, *Triceratops*

face and long supraorbital horns like a chasmosaurine. The Late Cretaceous *Pachyrhinosaurus*, notable for its hornlessness and presence of a massive nasal boss, was also controversial following its 1950 description. In studies of the 1960s and 70s, Wann Langston showed how *Triceratops* was an unusual member of Chasmosaurinae while *Pachyrhinosaurus* was an unusual member of Centrosaurinae. Studies published from 1990 onward have supported this work.

Since about 1994, a veritable cascade of new discoveries have added new branches and complexity to both the centrosaurine and chasmosaurine clades. Several discoveries show that centrosaurines started their history with long supraorbital horns, something we suspected given that ceratopsians close to ceratopsid ancestry—like *Zuniceratops*—have long supraorbital horns too.

Just one ceratopsid is known from outside of North America. This is *Sinoceratops* from the Late Cretaceous

of China. Because it belongs to an otherwise exclusively North American clade (the centrosaurines), it appears to show that a single migration event—involving movement from the Americas into Asia—occurred in the clade’s history. There is, however, the sneaking suspicion that it hints at a more complex history, and it may well be that more Asian ceratopsids await discovery.

See also Ceratopsians.

Ceratosaurs

A theropod group named for the horned Jurassic *Ceratosaurus* but argued at times to include the Triassic and Jurassic coelophysids, the Jurassic dilophosaurids, and the mostly Cretaceous abelisaurids and noosaurids. *Ceratosaurus* has been known since 1884. Some of its features (like its four-fingered hands and a row of bony nodules along the midline of its back) seem primitive, but others are advanced and birdlike. As a result, experts between the late 1800s and 1980s disagreed on its evolutionary position. Some allied it with megalosauroids, others with coelurosaurs, and others regarded it as an archaic theropod worthy of its own clade.

In his 1986 review of theropod phylogeny, Jacques Gauthier argued that *Ceratosaurus* and the abelisaurids belonged together with the coelophysids and dilophosaurids. The whole lot, he argued, were united by the presence of a bony shelf on the side of the thigh bone’s upper end, and by the presence of facial horns or crests. Gauthier co-opted a name for the group which Marsh had published in 1884—Ceratosauria—and proposed that Ceratosauria was a clade, and the sister-group of Tetanurae. This idea is interesting, since it would mean

that there were two contemporaneous theropod clades that descended from the same ancestor, one (Ceratosauria) more archaic than the other and with a distinctive facial look. A tempting analogy made more than once is that ceratosaurs might be imagined as the “marsupials” of the theropod world and tetanurans as the “placentals,” though don’t overthink this as it becomes less defensible the more you analyze it.

More recent studies have, alas, failed to support Gauthier’s view, and have instead found *Ceratosaurus* and abelisaurids to be closer to tetanurans than they are to coelophysids and dilophosaurids. Does this mean that we should abandon the name Ceratosauria? Well, maybe, but maybe not if a *Ceratosaurus* + abelisaurid clade exists, as some experts think it does. The fact that the name Ceratosauria has been used in different ways means, today, that any person using it has to explain which version of the term they have in mind.



Ceratosaurus was about 6 m (19.5 ft) long, and this in combination with its long teeth and large, deep skull show that it was a predator of large animals. The same was probably mostly true of the abelisaurids. Coelophysids (which were mostly 3–4 m [10–13 ft] long) were different, their shallow, narrow skulls and lightweight proportions suggesting they were predators of arthropods, small reptiles, and maybe fish. Dilophosaurids (6–7 m [19.5–23 ft] long) are built something like giant, heavily built coelophysids, and some experts have argued that this is exactly what they are. They're famous for their extravagant head gear. *Dilophosaurus* from the Early Jurassic of the southern USA has twinned, plate-like bony crests that might have been part of a larger, casque-like structure. *Cryolophosaurus* from the Early Jurassic of Antarctica has a vertical, fanlike crest formed of flattened, fingerlike bony projections above its eyes. Presumably these crests, horns, and other structures were used in display and communication, as are similar structures in modern birds and lizards.

See also Abelisaurids; Tetanurans.

Coelurosaurs

The enormous tetanuran clade that includes birds and other maniraptorans, ornithomimosaurs, and tyrannosauroids. The name Coelurosauria has a convoluted history which I can't begin to summarize here. But the modern concept of the term is rooted in Jacques Gauthier's proposal of 1986 that this name—first published by Friedrich von Huene in 1914—should be used for the clade containing all theropods closer to birds than to theropods like *Megalosaurus* and *Allosaurus*.

To Gauthier, this meant inclusion of the various small, agile theropods of the Late Jurassic—chicken-sized *Compsognathus* from Europe and *Ornitholestes* and *Coelurus* from the Morrison Formation—in addition to ornithomimosaurs and maniraptorans.

A series of studies published from the mid-1990s onward showed that tyrannosauroids should be included among this lot as well. Tyrannosauroids are substantially more birdlike than tetanurans like *Allosaurus* and must have evolved from small predators similar to *Coelurus*. In fact *Coelurus* (and other tetanurans of this sort) have always been imagined as the archetypal, ancestral coelurosaurs: as nimble, speedy, ground-running predators of the forest understorey, around 2 m (6.5 ft) long, equipped with long arms and three-fingered, grabbing hands. These *Coelurus*-like theropods were likely warm-blooded, so the idea that they might have been insulated by a feathery coat extends back to the 1970s. Fossils discovered since the 1990s have confirmed the presence of feathers on these animals, so feathers originated early in coelurosaur history, long before birds did. Presumably, their initial function was to retain heat, and only later did they become co-opted for use in flight and display.

At some point during the Early Jurassic (around 180 million years ago), some *Coelurus*-like coelurosaurs (certainly not *Coelurus* itself) evolved longer legs and necks and gave rise to ornithomimosaurs. Others began to rely on the strength of their jaws and teeth and were the earliest members of Tyrannosauroidea. Members of another lineage evolved longer arms and hands and smaller size and gave rise to maniraptorans. By the Late

Representatives of
some of the major
coelurosaurian groups



Jurassic, tens of coelurosaur species, representing numerous clades, inhabited the forests, prairies, deserts, and wetlands of the world, typically in environments where ceratosaurs, megalosauroids, and allosauroids were the big, dominant predators.

The Cretaceous might be imagined as the “Age of Coelurosaurs”: those other theropod groups were still around, but it was coelurosaurs which had evolved to fill the largest variety of ecological niches, the greatest variation in body size, and the most profound variation in body and skull shape. A lucky observer exploring a Late Cretaceous habitat in North America or Asia might have seen giant, omnivorous ornithomimosaurs, great, terrifying tyrannosauroids, and such maniraptorans as coyote-sized dromaeosaurids, ostrich-sized oviraptorosaurs, gigantic therizinosaurs, and some considerable diversity of birds.

See also Maniraptorans; Ornithomimosaurs; Tetanurans; Tyrannosauroids.

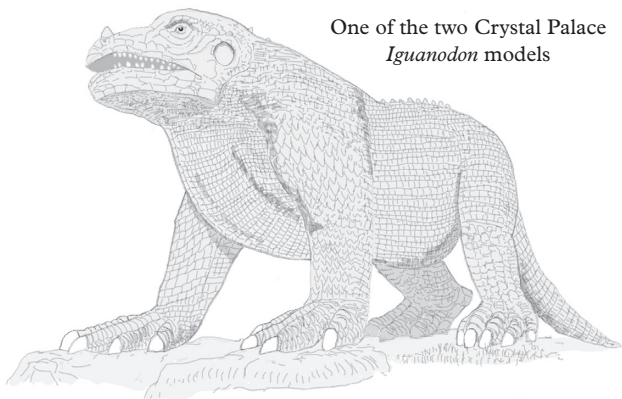
Crystal Palace

The south London park located in Penge (not Sydenham, as used to be stated), famous for its life-sized prehistoric animal models, all of which were constructed during the early 1850s. The models were part of a well-funded outreach project designed to accompany the relocation of the Crystal Palace building from Hyde Park (where it formed part of the Great Exhibition of 1851) to its new home on Penge Common. A landscaped, geology-themed park incorporating lakes, fountains, wooded areas, and gardens was constructed, and the models were sited on islands. Crystal Palace Park

remains in use today, but its appearance and function have changed substantially. The palace building burned down in 1936.

The models depict the three founding members of Dinosauria—*Megalosaurus*, *Iguanodon*, and *Hylaeosaurus*—as well as ichthyosaurs, plesiosaurs, pterosaurs, a mosasaur, and various animals of the Paleozoic and Cenozoic. Naturally, they're portrayed as per knowledge of the time, such that *Iguanodon* is a rhinocerotine quadruped with a nose horn, *Megalosaurus* is a sort of bear-crocodile-elephant mashup, and *Hylaeosaurus* is an iguana-like creature with a row of spines. It has occasionally been said or implied that the models are hilariously out of date. In reality, they were up to the minute at the time of construction, and should more sensibly be described as accurate, faithful representations of the scientific knowledge of the time. Their design and construction are owed entirely

One of the two Crystal Palace
Iguanodon models



to artist and sculptor Benjamin Waterhouse Hawkins, who was tasked with bringing to life the view of these animals described by Richard Owen. Owen gets credit as the scientific advisor, but exactly what role he played (beyond writing the guidebook) remains uncertain.

There's always been a modicum of historical interest in the Crystal Palace models. But only since the 1990s have those interested in artistic reconstructions of prehistoric animals paid detailed attention to their anatomy and the story of their construction. It's increasingly recognized that they're nuanced, fantastically detailed pieces of craftsmanship. This interest has gone hand-in-hand with efforts to see them and their grounds restored, cared for, valued, and celebrated. 2020 saw the installation of a bridge allowing improved access for maintenance, but also the continuing deterioration and vandalism of the models, specifically the ripping apart of the *Megalosaurus*' face by a member of the great British public.

See also Richard Owen.

D *einonychus*

Few non-bird dinosaurs can be considered as iconic as *Deinonychus antirrhopus*, a species named by John Ostrom in 1969 following discoveries made in the Lower Cretaceous Cloverly Formation of Montana, USA. Ostrom realized that *Deinonychus* was a member of Dromaeosauridae, a maniraptoran theropod clade named by William D. Matthew and Barnum Brown in 1922. Prior to Ostrom's work, dromaeosaurids were poorly understood and regarded as nondescript predators shaped like miniature tyrannosaurids.



Matthew and Brown actually regarded dromaeosaurids as a subgroup within Deinodontidae, this being their favored name for Tyrannosauridae.

Ostrom described *Deinonychus* as a mid-sized predator (it was around 3.5 m [11.5 ft] long and 60 kg [132 lbs]) with long hands, a flexible, birdlike wrist, a tail kept stiff by intertwined bony rods, and powerful hind limbs in which the second toe was arranged such that its enormous, strongly curved claw—the sickle claw—was kept raised off the ground. It was this claw which led Ostrom to give *Deinonychus*—meaning “terrible claw”—the name he did. He suggested that the sickle claw was a disemboweling weapon which *Deinonychus* deployed while standing on one leg and kicking with the other. Behavior of this sort requires agility and excellent balance, so here was evidence that some dinosaurs were dynamic, sprightly, hot-blooded predators. Robert Bakker’s illustration of *Deinonychus* in mid-stride, produced to accompany Ostrom’s 1969 description of this dinosaur, helped put it front and center in every discussion of the Dinosaur Renaissance.

Because the remains of several *Deinonychus* individuals had been discovered together, Ostrom further proposed that *Deinonychus* was a group-living pack-hunter that ganged up to kill big dinosaurs, the rhinocerosized ornithomimid *Tenontosaurus* being—in his view—*Deinonychus*'s most favored item of prey.

Today we know that Ostrom wasn't, actually, the first to "discover" *Deinonychus*. Bones of the exact same animal were discovered by Barnum Brown and Peter Kaisen on an American Museum of Natural History expedition of 1931, and Brown went as far as having a skeletal reconstruction prepared for a planned publication. His working name for this animal was *Daptosaurus agilis*. But, alas, he never got around to finishing this work . . . a problem that any working scientist knows all too well.

Deinonychus hasn't become notably better known since the publication of Ostrom's 1969 monograph, bar the appearance of new work on its palate, snout shape, and hand orientation. Dromaeosaurid fossils from China show that dromaeosaurids large and small were fully feathered, with a plumage much like that of *Archaeopteryx* and other archaic birds. Their forelimbs were winglike and oriented such that the palms were fixed in an inward-facing pose. All these things would have been true of *Deinonychus*. It would have looked more like a giant, striding, long-tailed hawk than anything else.

Ostrom's views on the behavior and lifestyle of this dinosaur have also undergone revision. Sickie-shaped claws aren't, it turns out, built for slicing or slashing at giant animals, but for gripping or pinning small ones.

Ostrom's view that *Deinonychus* was a pack-hunter has been the source of considerable debate. Some experts have outright stated that group hunting wasn't likely for these animals (it's more of a mammalian habit than a reptilian one, so the argument goes), nor is it well supported by geological data, since the individuals Ostrom regarded as members of a social group more likely came together by accident (they were washed together by floodwater, say). But none of this appears exactly right; social behavior is reasonably well supported in these animals and can't be easily explained away, *Deinonychus* isn't the only dromaeosaurid where several individuals have been discovered in association, and the diversity of group-hunting strategies present in modern lizards and birds shows that cooperation and group living are far from "mammal-only" behaviors. It's plausible that *Deinonychus* sometimes hunted alone, but it's also likely that individuals stalked and foraged in bands, cooperated in the flushing and pursuing of prey like small ornithischians, and slept and nested in groups.

See also Robert Bakker; Dinosaur Renaissance; John Ostrom; Maniraptorans; Raptor Prey Restraint.

Dinosaur Renaissance

The cultural event of the 1960s and 70s (though read on) in which dinosaurs were recast as agile, social, warm-blooded, successful animals that live on as birds. Those promoting this view of dinosaurs—predominantly John Ostrom and his student Robert Bakker—disputed the stereotype prevalent beforehand: that dinosaurs were monuments of inefficiency and bad design, destined for extinction. Bakker termed this overturning of ideas

a Renaissance, his argument being that it marked a return to a more vigorous view of dinosaurs prevalent during the late 1800s.

The Renaissance made dinosaurs attractive areas of discussion, and heated exchanges on their biology occurred in scientific journals. Adrian Desmond's 1975 book *The Hot-Blooded Dinosaurs* did much to popularize the Renaissance, as did articles in *Scientific American*, *National Geographic*, and *Discovery*.

The Dinosaur Renaissance is usually implied to result from Bakker's and Ostrom's efforts alone, the main catalysts being Bakker's articles (published between 1968 and 1974) on dinosaur "warm-bloodedness" and the terrestrial lifestyle of sauropods, and Ostrom's 1969 description of *Deinonychus*. But an alternative take on the Renaissance might be that it was the inevitable consequence of post-WWII history and generational turnover. The ideas Ostrom and Bakker promoted were based mostly on fossils—like those discovered during the Polish-Mongolian expeditions of the 1960s and 70s—whose discovery and study could only happen within the decades following WWII. Furthermore, the postwar baby boom resulted in the existence of a generation the right age to be intrigued by, and engage with, the implications of these fossils. Such topics as the origin of birds, dinosaur behavior, and dinosaur feeding mechanisms had *always* been the topic of investigation, it's just that the number of studies published prior to the 60s and 70s had been low due to a small number of publishing paleontologists. Take all of this into consideration, and a fairer appraisal of the Renaissance might be that it occurred as a perfect storm of events.

If the Renaissance was a cultural “event,” when did it end? Was it short-lived and ended during the 70s, was it more drawn-out, or is it that we’re still in it? I invited the thoughts of colleagues on this matter and discovered a diversity of opinions. The fact that we remain in a dynamic, fast-moving period whereby the ideas of the Renaissance continue to be supported and investigated *could* mean that the Renaissance is still ongoing.

But I rather prefer the view that the Renaissance could be considered “finished” once Renaissance views of dinosaurs became accepted in mainstream culture. The 1993 appearance of *Jurassic Park* could be interpreted as marking that acceptance, as could the 1990s publication of feathered dinosaurs like *Sinosauropteryx* and *Caudipteryx*. And if the Renaissance *has* finished, maybe we’re now in a new period, a sort of *Dinosaur Enlightenment*.

See also Robert Bakker; *Deinonychus*; John Ostrom.

Dinosauroid

The idea that life on Earth might be very different had non-bird dinosaurs not died out is a familiar staple of science fiction. But it’s one that’s also been explored by scientists and science writers. From 1969 onward, Canadian paleontologist Dale Russell (1937–2019) published a series of papers on troodontids, a group of maniraptorans notable for their proportionally large brains (well, large for non-bird dinosaurs). Russell was especially interested in the evolution of intelligence, the possible existence of alien life, and the Search for Extraterrestrial Intelligence (or SETI) project.

What, he wondered, might troodontids look like had they not become extinct 66 million years ago? Russell explored this speculation in a 1982 article, coauthored with Canadian Museum of Nature model maker and taxidermist Ron Séguin. Séguin had been tasked with the construction of a life-sized model of a troodontid, and through collaboration with Russell he also built a hypothetical troodontid descendant. Russell and Séguin proposed that troodontids would have evolved a larger brain had they persisted beyond the Creta-

ceous, and that this would have led to an erect posture, reduced tail, and humanoid form. They called the resulting creature the dinosauroid.



Feelings on the dinosauroid have run in two directions. On the one hand, there are those who've argued that convergent evolution is so pervasive, and the human form so effective a design, that the evolution of humanoid dinosaurs is plausible, perhaps even likely or inevitable. Such has been promoted by evolutionary scientists and authors Simon Conway-Morris and

Richard Dawkins. On the other hand, another group (mostly paleontologists who specialize in dinosaurs) have argued that Russell's underlying premise—that troodontids would become humanoid had they evolved larger brains—is flawed, since a big-brained maniraptoran would remain maniraptoran-like, not head in a humanoid direction of evolution.

Dinosauroid-like creatures had been portrayed innumerable times before Russell and Séguin's project. Examples include the Mahars and Horibs of Edgar Rice Burroughs' writings, the Silurians of *Doctor Who*, and the Sleestaks of *Land of the Lost*. There is, however, no indication that any of these were inspirational to the dinosauroid. Others appeared afterward, sometimes as homages, but sometimes (as with Harry Harrison's Yilané from 1984's *West of Eden*) to show that the author could portray more "plausible" smart reptiles. Since about 2014, numerous artists have invented their own "dinosauroids," most of which are feathery, horizontal-bodied animals which more resemble maniraptorans than scaly green humanoids.

There are indications that Russell was unhappy with the mostly negative reception the dinosauroid received, and it might be that it damaged his credibility. However, the primary aim of the project was to encourage discussion of the idea that the humanoid form could be evolved by other forms of life, the concluding words of his and Séguin's 1982 paper being "We invite our colleagues to identify alternative solutions." Seen from this point of view, the experiment was a major success. The dinosauroid has remained a touchstone of discussions

on speculative evolution, numerous copies of Séguin's model exist, and few people interested in dinosaurs are unaware of it.

See also Maniraptorans.

Diplodocoids

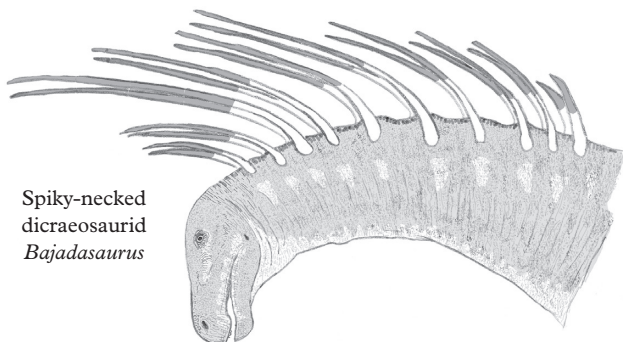
The sauropod clade which includes the archaic rebbachisaurids and the whip-tailed dicraeosaurids and diplodocids. Key features uniting all three include slender tooth crowns and short, non-overlapping ribs on the neck vertebrae. A typical diplodocoid has an especially long neck and tail, and a lightweight, long, shallow-snouted skull with a squared-off mouth. The skulls of some rebbachisaurids are unusual in that the end of the snout is the widest part, and the only part to contain teeth. The whiplike tail tips of dicraeosaurids and diplodocids likely served an offensive or defensive function.

The best known diplodocoids are the Morrison Formation animals *Diplodocus*, *Barosaurus*, *Apatosaurus* and *Brontosaurus*, all of which belong to Diplodocidae. They include some of the largest of dinosaurs, some exceeding 25 m (82 ft) in length. Possibly even bigger is *Maraapunisaurus*, also of the Morrison Formation. Its now lost remains suggest a length of more than 30 m (98 ft). *Maraapunisaurus* was long regarded as a diplodocid but has recently been reidentified as a rebbachisaurid.

A few aspects of diplodocoid biology and behavior remain the topic of argument. The presence in diplodocids of relatively short forelimbs, tall vertebral spines in the hip region, and an aft-located center of mass (plus

other features) have led some researchers to argue that members of this specific group were good at standing in a bipedal or tripodal pose. Maybe they did this to reach high up into foliage, when fighting, or when intimidating or battling big theropods. The habitual neck pose of these animals is also debated. Some researchers argue that diplodocoid necks were constrained to a horizontal pose, perhaps with an upward or even downward curve at the head end, while others (including myself) think that the necks were ordinarily held mostly erect. Add these things together and we come to a third area of argument: feeding behavior. Did diplodocoids use their ultra-long necks to reach down to the ground to crop ferns, horsetails and cycads, or were they more adept at reaching up, beyond the reach of other herbivores and into the canopy? My take is that they were doing both of these things as and when required, their behavior changing from one species to the next as well as across their life span. Claims that erect neck poses would be disallowed by blood pressure are naive given that the sauropod neck—a structure some order of magnitude bigger than that present in living animals—almost certainly involved the existence of remarkable soft tissue specializations.

Diplodocoids are associated mostly with the Late Jurassic; however, the Chinese dicraeosaurid *Lingwulong* shows that they'd diversified into their three major groups prior to the Middle Jurassic. Despite this, rebbachisaurids are predominantly Cretaceous (*Maraapunisaurus* being an exception). The relatively short necks, downcurved snouts, and wide mouths of rebbachisaurids might show that they were specialized ground-level



Spiky-necked
dicraeosaurid
Bajadasaurus

feeders. Both diplodocids and dicraeosaurids persisted into the Cretaceous in South America, and among the last of them were the remarkable dicraeosaurids *Bajadasaurus* and *Amargasaurus*, both of Argentina. Long bony spines, projecting upward from the neck vertebrae, were probably sheathed in horn and perhaps used in visual display.

See also *Brontosaurus*; Morrison Formation; Sauropods.

H adrosaur Nesting Colonies

By the 1970s, it was well established that non-bird dinosaurs constructed nests where they deposited their oval or near-spherical eggs. This was demonstrated by fossil eggs and nests found in various locations, most famously those found during the 1920s in the Late Cretaceous rocks of Mongolia. There were, however, no clear ideas on whether non-bird dinosaurs practiced parental care, whether their nesting was a solitary or social affair, or whether they had a preference

with respect to the nesting sites they chose. The fact that Mesozoic dinosaur eggs and nests were rare led to the belief that nesting behavior was restricted to upland places, but why babies were so rare remained enigmatic.

This changed during the late 1970s and throughout the 80s as studies led by Jack Horner announced a series of finds made in western Montana, USA. In 1978, Horner and his friend and colleague Bob Makela visited the small Montana town of Bynum. At a rock and fossil shop owned by Marion Brandvold, they were asked to identify some small bones. These turned out to be baby hadrosaur bones from an animal around 45 cm (1.5 ft) long, the first of a string of amazing discoveries.

The bones came from the sediments of the Two Medicine Formation, a Late Cretaceous layer about 77 million years old. After exploring the exact spot where Brandvold had found them, Horner and Makela discovered a bunch more (representing another 14 individuals), all jumbled together, preserved in what had originally been a circular depression on top of a mound. Eggshell fragments were associated with the bones. This was a hadrosaur nest, and the remains belonged to a new kind of hadrosaur, which they named *Maiasaura* (meaning “good mother lizard”) in 1979. The skull of an adult was found about 100 m (328 ft) away. Because the babies had died in the nest, Horner and Makela proposed that parental care existed, but that this unfortunate lot had starved to death after one or both parents failed to return.

In subsequent studies, Horner reported the presence of an additional six or so *Maiasaura* nests at the same site, all spaced around 7 m (23 ft) apart. Here was

evidence that this hadrosaur—and presumably hadrosaurs in general—nested in colonies. The timing of these discoveries was ideal, since they were announced while writers and journalists were still reeling from the implications of the Dinosaur Renaissance. Here was evidence that non-bird dinosaurs were behaviorally complex and even birdlike in breeding behavior. The consequence is that *Maiasaura* gets its own section in virtually every single post-1979 book or article on dinosaurs, and that *Maiasaura* and its cute, short-snouted babies are among the most frequently illustrated of all hadrosaurs.

Horner's model for nesting and parental behavior in *Maiasaura* is that these animals gathered in colonies to nest, constructed crater-shaped nests in which a clutch of 20–30 eggs were incubated by rotting vegetation, that one or both parents brought food to the hatchlings, and that the hatchlings stayed in the nest until they were around 1 m (3 ft) long. Subsequent discoveries made elsewhere—including other locations in Montana and Devil's Coulee in Alberta, Canada—have supported this model of colonial nesting and parental care, and in fact colonial nesting has since been documented for sauropods and non-bird theropods too.

See also Dinosaur Renaissance; Hadrosaurs; Jack Horner.

Hadrosaurs

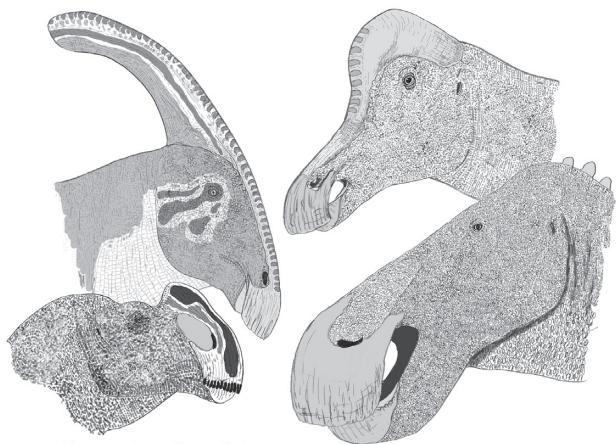
Among the most abundant, widespread, and best understood of non-bird dinosaur clades. Hadrosaurs—often termed duck-billed dinosaurs or duck-bills (though read on)—are a mostly Late Cretaceous clade

of iguanodontian ornithopods. They belong to a larger group (termed Hadrosauroidea) which evolved from big, *Iguanodon*-like quadrupeds.

Hadrosaurs were mostly large or very large herbivores, species ranging from 4 m (13 ft) to an incredible 17 m (56 ft) in the gigantic *Shantungosaurus* of eastern China. They were equipped with robust hind limbs with three-toed feet, a muscular tail that was stiff and shallow in its end half, and specialized hands where the thumb was absent, the middle three digits were united in a pseudohoof, and the fifth finger was rodlike and independently mobile. The hadrosaurian skull combines a toothless, beaked region with massive tooth batteries. Their teeth, cemented together for strength, underwent constant replacement. Around 1,000 teeth were present in some species, and histological work shows that they're among the most complex teeth that have ever evolved.

Hadrosaurs are diverse in skull anatomy. There are long-faced, crestless taxa, those with deep, arched nasal regions, a clade with solid, spike-shaped bony crests and another with hollow bony crests that have a complex architecture. One fossil seems to show that even taxa lacking bony crests might have had soft, fleshy crests. Dismissive claims that hadrosaurs are all the same bar skull shape are dead wrong: there's considerable variation in their proportions, limb bone shapes and much else.

Within recent decades, the consensus has been to regard hadrosaurs as a clade (termed Hadrosauridae) that contains two additional, internal clades: the flat-headed and solid-crested Hadrosaurinae, and the hollow-crested Lambeosaurinae. Additional



subdivisions within both of these clades have been recognized as well. Within Hadrosaurinae, the clades Brachylophosaurini, Edmontosaurini, Kritosaurini, and Saurolophini are recognized. Meanwhile, Lambeosaurinae contains Aralosaurini, Tsintaosaurini, Parasaurolophini, and Lambeosaurini.

A complication arose in 2010, however, when hadrosaur expert Alberto Prieto-Marquez discovered that *Hadrosaurus* from New Jersey—the namesake member of the group (and among the first of North American non-bird dinosaurs to be named)—belongs outside the clade that contains most other hadrosaurs. This means that the name Hadrosaurinae can't be applied to the group conventionally given that name. Saurolophinae (originally published in 1918) is available as an alternative, and Prieto-Marquez and his colleagues endorse the use of “saurolophine” in place of “hadrosaurine.”

Another complication worth mentioning is Jack Horner's idea, proposed during the early 1990s, that saurolophines and lambeosaurines have distinct ancestry and that the former descend from *Iguanodon*-like ancestors, while the latter evolved from *Ouranosaurus*-like animals (*Ouranosaurus* is a sail-backed iguanodontian from the Early Cretaceous of Niger). This hasn't been supported by more recent studies.

The flattened, broad snout of saurolophines like *Edmontosaurus* explains why these dinosaurs have often been described as "duck-billed" ("spoon-billed" has also been used). Hadrosaurs like *Edmontosaurus* do, it's true, have a skull that looks spatulate when viewed from above or below. But exceptional specimens with their keratinous beak tissue preserved show that this spatulate anatomy was obscured in life, and that a massive down-curved bill was instead the dominant feature. This configuration was correctly described by Jan Verduyn in 1923 and again by William Morris in 1970 but mostly ignored until recently.

This massive bill was used in cropping foliage of all sorts. When we combine its anatomy with that of the tooth batteries, it appears that hadrosaurs were unstoppable, incredible destroyers of plants, able to break apart and consume leaves, fronds, stems, branches, and even wood. A diet involving all these items—as well as occasional animal matter, like crustacean parts—is confirmed by fossil hadrosaur dung. An old-fashioned idea that hadrosaurs were amphibious and limited to a diet of soft water-plants therefore has a lot counting against it. It does, however, remain possible that hadrosaurs were good waders or swimmers, and it might be that

some taxa consumed amphibious or aquatic plants on a regular basis. But hadrosaur anatomy shows mostly that they were terrestrial animals of wooded places and even scrub and semidesert. When it comes to other aspects of biology, we know much about hadrosaur nesting behavior thanks to eggs, nests, and nesting grounds discovered in the USA.

Hadrosaurs are associated mostly with North America and Asia, but taxa are also known from South America, Europe, Antarctica, and northern Africa. This distribution is consistent with a mid-Cretaceous origin in eastern Asia followed by a series of dispersals to other regions, some of which likely involved over-water crossings (or swimming, as it's more generally known).

See also Hadrosaur Nesting Colonies; *Iguanodon*; Ornithopods.

Hell Creek

Among those locations associated with dinosaur-bearing sedimentary layers, few are as famous as Hell Creek, Montana. Why? Well, hold on, we'll come to that in a minute. Hell Creek is characterized by badlands topography, a landscape where dry gullies and steep slopes have formed by wind and water erosion. The sediments here—consisting of mudstones, siltstones, and sandstones—date to the Late Cretaceous and Paleocene, but it's the Cretaceous layers that are of direct interest to us. They're from the Maastrichtian (the very final geological stage of the Late Cretaceous) and belong to a set of sediments that extend over part of North and South Dakota and Wyoming in addition to Montana.

Famous paleontologist Barnum Brown was the first to recognize these sediments as worthy of a name: in 1907, he named them the Hell Creek beds. But in the years that followed, experts mostly regarded the Hell Creek sediments as part of the Lance Formation. The term Hell Creek Formation came into use during the 1950s but wasn't formally established until 2014. The terms Hell Creek and Hell Creek Formation are not technically synonymous, but it's common in discussions of Late Cretaceous life to refer to all the animals of the Hell Creek Formation as belonging to the Hell Creek fauna.

The main reason for Hell Creek's fame comes from the fact that this is the area in which the *Tyrannosaurus rex* holotype (the key specimen regarded as the one associated with the name) was discovered back in 1902, though it has to be said that the memorable name is surely a factor as well. "Hell Creek" is fitting for a place associated with an animal often regarded as the world's most awesome apex predator. In addition to *T. rex*, the Hell Creek fauna includes *Triceratops*, *Ankylosaurus*, *Pachycephalosaurus*, and the hadrosaur *Edmontosaurus*, all of which can be considered the final, "ultimate" members of their respective clades.

But it's not all dinosaurs. Plant fossils provide a good impression of what the place was like during Maastrichtian times, and numerous fishes, amphibians, mammals, lizards, turtles, and invertebrates are known from Hell Creek sediments too. This was a densely forested, subtropical or temperate lowland during the Maastrichtian, with a hot rainy season and cool dry season. Animals like *T. rex* stalked forests and fern prairies, but swamps

and rivers occurred in the region and the area was entirely swampy at times. The proximity of the receding Western Interior Seaway meant that estuarine conditions were present to the south and east, and marine animals sometimes entered local rivers.

The significance of the Hell Creek Formation to the study of Mesozoic geology and paleontology is reflected by the fact that the Hell Creek Fossil Area was designated a National Natural Landmark by the National Park Service in 1966. Fieldwork in Hell Creek continues today, and work on its fossils, sedimentology, and stratigraphy appears regularly in the scientific press. Furthermore, its animals, plants and environments are unusually well represented in paleoart, and artists have gone to considerable trouble to portray things accurately.

See also *Tyrannosaurus rex*.

Herrerasaurs

One of the most archaic dinosaur groups, a predatory, theropod-like clade of Late Triassic South America, and probably North America, Europe, and India. Herrerasaurs (properly *Herrerasauridae*) became known in 1973 when *Herrerasaurus* was described from Argentina. It was initially suspected to be a prosauropod. Excellent remains described in the 1990s show that *Herrerasaurus* had a rectangular snout, long, recurved teeth, and theropod-like forelimbs. Large claws are present on the inner three fingers, and the mobility of the wrist and elbow is similar to that of tetanurans. *Herrerasaurus* is the largest member of the clade, in cases reaching 6 m (19.5 ft). Other herrerasaurs—they include