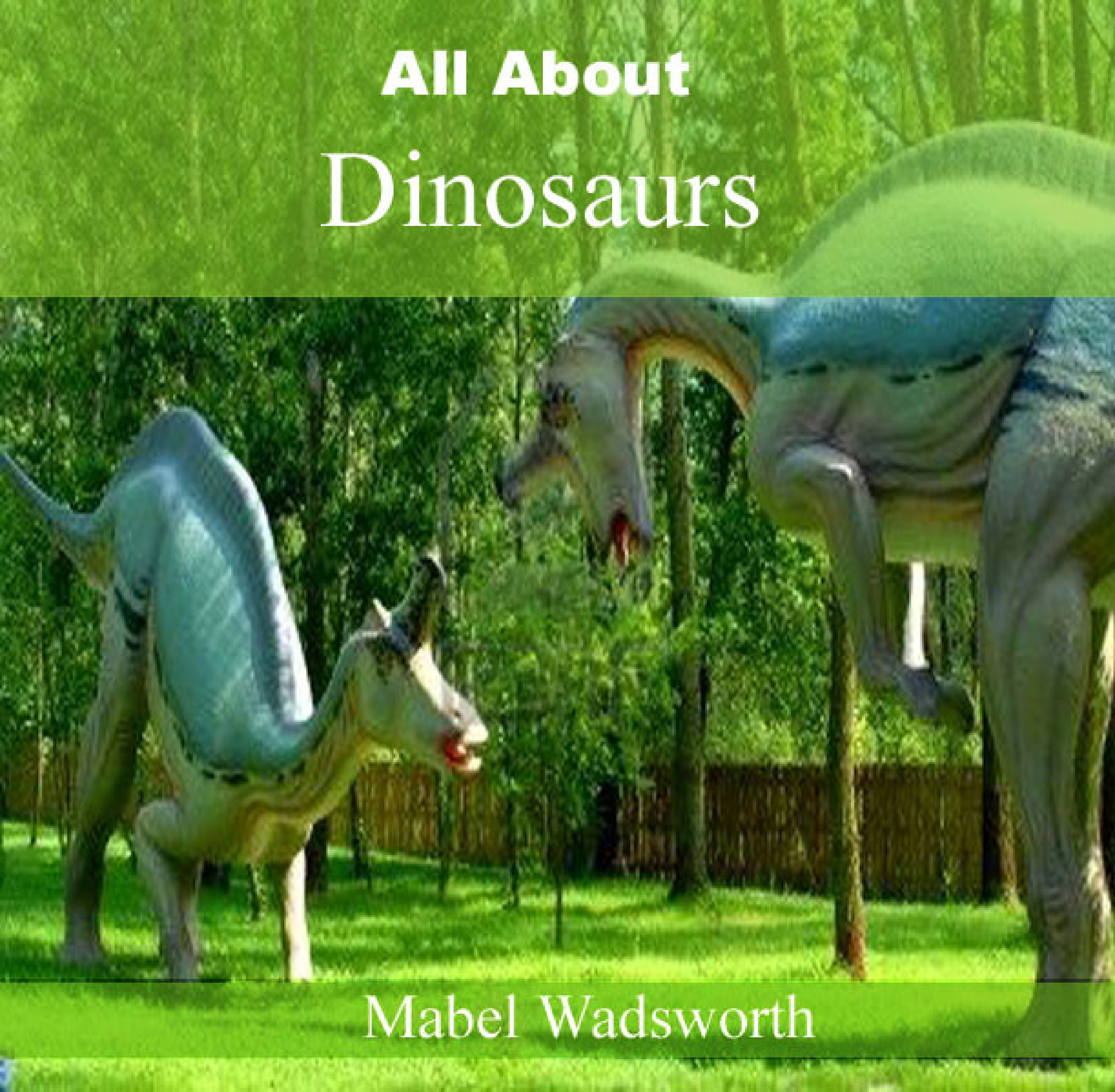

All About Dinosaurs

Mabel Wadsworth

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Table of Contents

Chapter- 1

Dinosaur

Dinosaurs

Fossil range:

Late Triassic-Late Cretaceous, 231.4–65.5 Ma

Descendant taxon Aves survives to present

Mounted skeletons of *Tyrannosaurus* (left) and *Apatosaurus* (right) at the American Museum of Natural History

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Reptilia
(unranked):	Ornithodira
(unranked):	Dinosauromorpha
(unranked):	Dinosauriformes
Superorder:	**Dinosauria** Owen, 1842

Orders and suborders

- **†Ornithischia**

    - †Cerapoda
    - †Thyreophora
- **Saurischia**
    - †Sauropodomorpha
    - Theropoda

Dinosaurs are a diverse group of animals that were the dominant terrestrial vertebrates for over 160 million years, from the late Triassic period (about 230 million years ago) until the end of the Cretaceous (about 65 million years ago). The extinction of most dinosaur species occurred during the Cretaceous–Tertiary extinction event. The fossil record indicates that birds evolved within theropod dinosaurs during the Jurassic period. Some of them survived the Cretaceous–Tertiary extinction event, including the ancestors of all modern birds. Consequently, in modern classification systems, birds are considered a type of dinosaur—the only group of which that has survived to the present day.

Dinosaurs are a diverse and varied group of animals; birds, at over 9,000 species, are the most diverse group of vertebrate besides perciform fish. Paleontologists have identified over 500 distinct genera and more than 1,000 different species of non-avian dinosaurs. Dinosaurs are represented on every continent by both extant species and fossil remains. Some dinosaurs are or were herbivorous, others carnivorous. Some have been bipedal, others quadrupedal, and others have been able to shift between these body postures. Many non-avian species developed elaborate skeletal modifications such as bony armor, horns or crests. Avian dinosaurs have been the planet's dominant flying vertebrate since the extinction of the pterosaurs. Although generally known for the large size of some species, most dinosaurs were human-sized or even smaller. Most groups of dinosaurs are known to have built nests and laid eggs.

The term "dinosaur" was coined in 1842 by the English paleontologist Richard Owen, and derives from Greek *δεινός* (*deinos*) "terrible, powerful, wondrous" + *σαῦρος* (*sauros*) "lizard". Through the first half of the twentieth century, most of the scientific community believed dinosaurs to have been sluggish, unintelligent cold-blooded animals. Most research conducted since the 1970s, however, has indicated that dinosaurs were active animals with elevated metabolisms and numerous adaptations for social interaction.

Since the first dinosaur fossils were recognized in the early nineteenth century, mounted dinosaur skeletons have been major attractions at museums around the world, and dinosaurs have become a part of world culture. They have been featured in best-selling books and films such as *Jurassic Park*, and new discoveries are regularly covered by the media. In informal speech, the word "dinosaur" is used to describe things that are impractically large, slow-moving, obsolete, or bound for extinction, reflecting the outdated view that dinosaurs were maladapted monsters of the ancient world.

Etymology

The taxon **Dinosauria** was formally named in 1842 by Sir Richard Owen, who used it to refer to the "distinct tribe or sub-order of Saurian Reptiles" that were then being recognized in England and around the world.[:103] The term is derived from the Greek words δεινός (*deinos* meaning "terrible", "powerful", or "wondrous") and σαῦρος (*sauros* meaning "lizard" or "reptile").[:103] Though the taxonomic name has often been interpreted as a reference to dinosaurs' teeth, claws, and other fearsome characteristics, Owen intended it merely to evoke their size and majesty. In colloquial English "dinosaur" is sometimes used to describe an obsolete or unsuccessful thing or person, despite the dinosaurs' 160 million year reign and the global abundance and diversity of their avian descendants: modern-day birds.

Modern definition

Triceratops skeleton at the American Museum of Natural History in New York City

Under phylogenetic taxonomy, dinosaurs are usually defined as the group consisting of "*Triceratops*, Neornithes [modern birds], their most recent common ancestor, and all descendants." It has also been suggested that Dinosauria be defined with respect to the most recent common ancestor of *Megalosaurus* and *Iguanodon*, because these were two of the three genera cited by Richard Owen when he recognized the Dinosauria. Both definitions result in the same set of animals being defined as dinosaurs, including theropods (mostly bipedal carnivores), sauropodomorphs (mostly large herbivorous quadrupeds with long necks and tails), ankylosaurians (armored herbivorous quadrupeds), stegosaurians (plated herbivorous quadrupeds), ceratopsians (herbivorous quadrupeds with horns and frills), and ornithopods (bipedal or quadrupedal herbivores including "duck-bills"). These definitions are written to correspond with scientific conceptions of dinosaurs that predate the modern use of phylogenetics. The continuity of meaning is intended to prevent confusion about what the term "dinosaur" means.

There is a wide consensus among paleontologists that birds are the descendants of theropod dinosaurs. Using the strict cladistical definition that all descendants of a single common ancestor must be included in a group for that group to be natural, birds would thus *be* dinosaurs and dinosaurs are, therefore, not extinct. Birds are classified by most paleontologists as belonging to the subgroup Maniraptora, which are coelurosaurs, which are theropods, which are saurischians, which are dinosaurs.

From the point of view of cladistics, birds are dinosaurs, but in ordinary speech the word "dinosaur" does not include birds. Additionally, referring to dinosaurs that are not birds as "non-avian dinosaurs" is cumbersome.

General description

Stegosaurus skeleton, Field Museum, Chicago

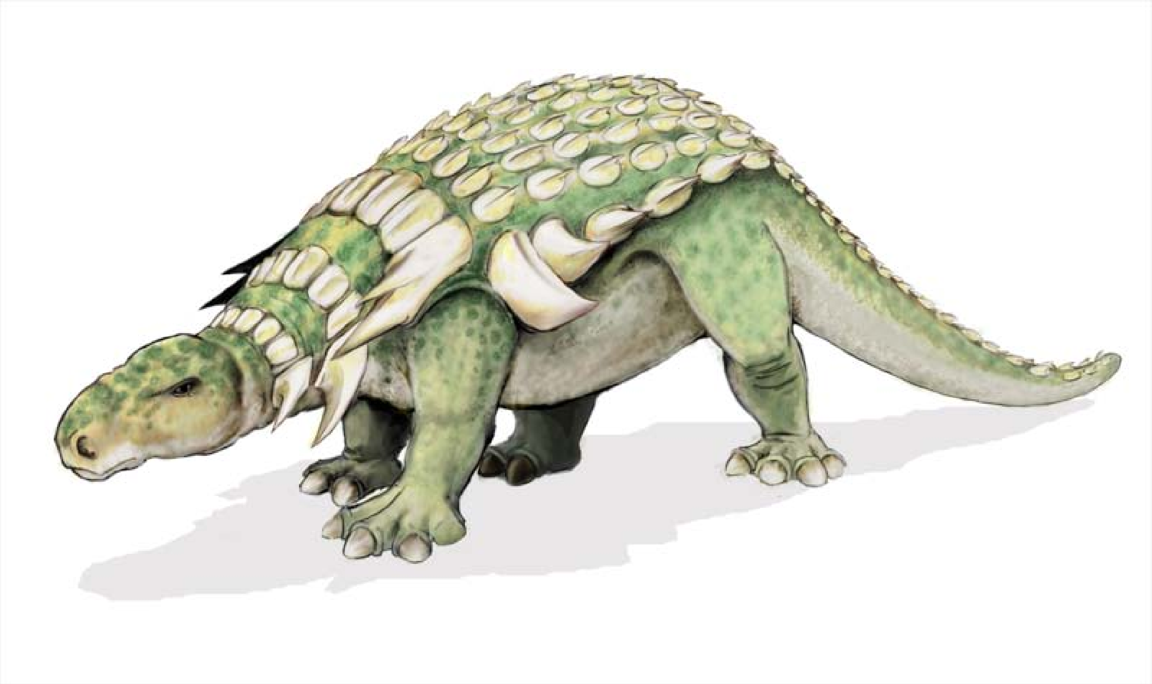
Using one of the above definitions, dinosaurs (aside from birds) can be generally described as terrestrial archosaurian reptiles with limbs held erect beneath the body, that existed from the Late Triassic (first appearing in the Carnian faunal stage) to the Late Cretaceous (going extinct at the end of the Maastrichtian). Many prehistoric animals are popularly conceived of as dinosaurs, such as ichthyosaurs, mosasaurs, plesiosaurs, pterosaurs, and *Dimetrodon*, but are not classified scientifically as dinosaurs. Marine reptiles like ichthyosaurs, mosasaurs, and plesiosaurs were neither terrestrial nor archosaurs; pterosaurs were archosaurs but not terrestrial; and *Dimetrodon* was a Permian animal more closely related to mammals. Dinosaurs were the dominant terrestrial vertebrates of the Mesozoic, especially the Jurassic and Cretaceous. Other groups of animals were restricted in size and niches; mammals, for example, rarely exceeded the size of a cat, and were generally rodent-sized carnivores of small prey. One notable exception is *Repenomamus giganticus*, a triconodont weighing between 12 kilograms (26 lb) and 14 kilograms (31 lb) that is known to have eaten small dinosaurs like young *Psittacosaurus*.

Dinosaurs were an extremely varied group of animals; according to a 2006 study, over 500 dinosaur genera have been identified with certainty so far, and the total number of genera preserved in the fossil record has been estimated at around 1850, nearly 75% of which remain to be discovered. An earlier study predicted that about 3400 dinosaur genera existed, including many which would not have been preserved in the fossil record. As of September 17, 2008, 1047 different species of dinosaurs have been named. Some were herbivorous, others carnivorous. Some dinosaurs were bipeds, some were quadrupeds, and others, such as *Ammosaurus* and *Iguanodon*, could walk just as easily on two or four legs. Many had bony armor, or cranial modifications like horns and crests. Although known for large size, many dinosaurs were human-sized or smaller. Dinosaur remains have been found on every continent on Earth, including Antarctica. No dinosaurs are known to have lived in marine or aerial habitats, although it is possible some feathered theropods were flyers. There is also evidence that some spinosaurids had semi-aquatic habits.

Distinguishing anatomical features

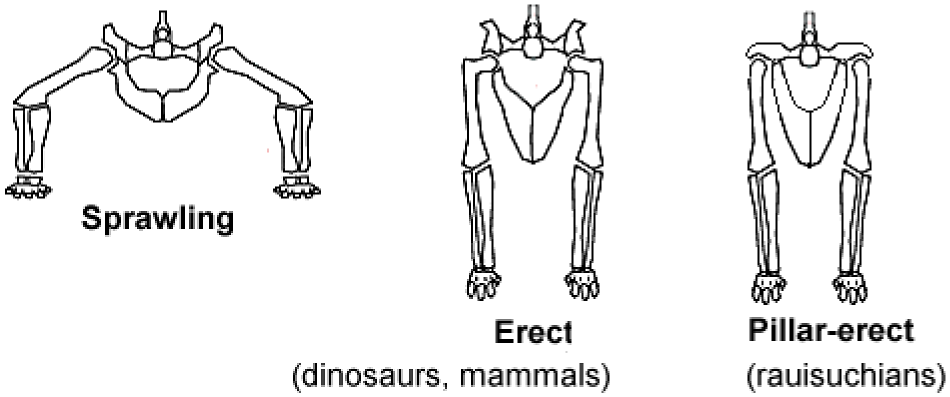
While recent discoveries have made it more difficult to present a universally agreed-upon list of dinosaurs' distinguishing features, nearly all dinosaurs discovered so far share certain modifications to the ancestral archosaurian skeleton. Although some later groups of dinosaurs featured further modified versions of these traits, they are considered typical across Dinosauria; the earliest dinosaurs had them and passed them on to all their descendants. Such common features across a taxonomic group are called synapomorphies.

Dinosaur synapomorphies include an elongated crest on the humerus, or upper arm bone, to accommodate the attachment of deltopectoral muscles; a shelf at the rear of the ilium, or main hip bone; a tibia, or shin bone, featuring a broad lower edge and a flange pointing out and to the rear; and an ascending projection on the astragalus, one of the ankle bones, which secures it to the tibia.



Edmontonia was an armored dinosaur of the group Ankylosauria

A variety of other skeletal features were shared by many dinosaurs. However, because they were either common to other groups of archosaurs or were not present in all early dinosaurs, these features are not considered to be synapomorphies. For example, as diapsid reptiles, dinosaurs ancestrally had two pairs of temporal fenestrae (openings in the skull behind the eyes), and as members of the diapsid group Archosauria, had additional openings in the snout and lower jaw. Additionally, several characteristics once thought to be synapomorphies are now known to have appeared before dinosaurs, or were absent in the earliest dinosaurs and independently evolved by different dinosaur groups. These include an elongated scapula, or shoulder blade; a sacrum composed of three or more fused vertebrae (three are found in some other archosaurs, but only two are found in *Herrerasaurus*); and an acetabulum, or hip socket, with a hole at the center of its inside surface (closed in *Saturnalia*, for example). Another difficulty of determining distinctly dinosaurian features is that early dinosaurs and other archosaurs from the Late Triassic are often poorly known and were similar in many ways; these animals have sometimes been misidentified in the literature.

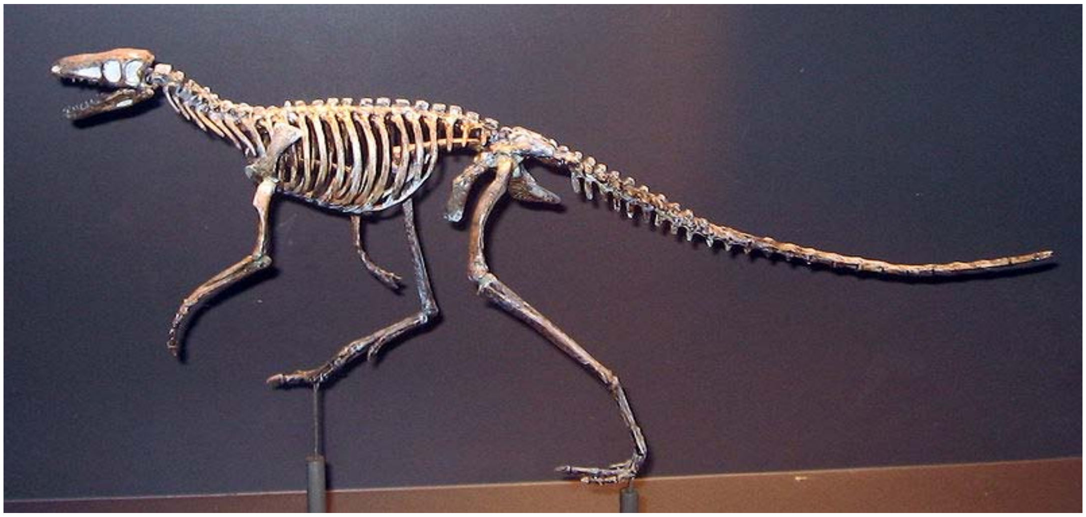


Hip joints and hindlimb postures

Dinosaurs stood erect in a manner similar to most modern mammals, but distinct from most other reptiles, whose limbs sprawl out to either side. Their posture was due to the development of a laterally facing recess in the pelvis (usually an open socket) and a corresponding inwardly facing distinct head on the femur. Their erect posture enabled dinosaurs to breathe easily while moving, which likely permitted stamina and activity levels that surpassed those of "sprawling" reptiles. Erect limbs probably also helped support the evolution of large size by reducing bending stresses on limbs. Some non-dinosaurian archosaurs, including rauisuchians, also had erect limbs but achieved this by a "pillar erect" configuration of the hip joint, where instead of having a projection from the femur insert on a socket on the hip, the upper pelvic bone was rotated to form an overhanging shelf.

Natural history

Origins and early evolution

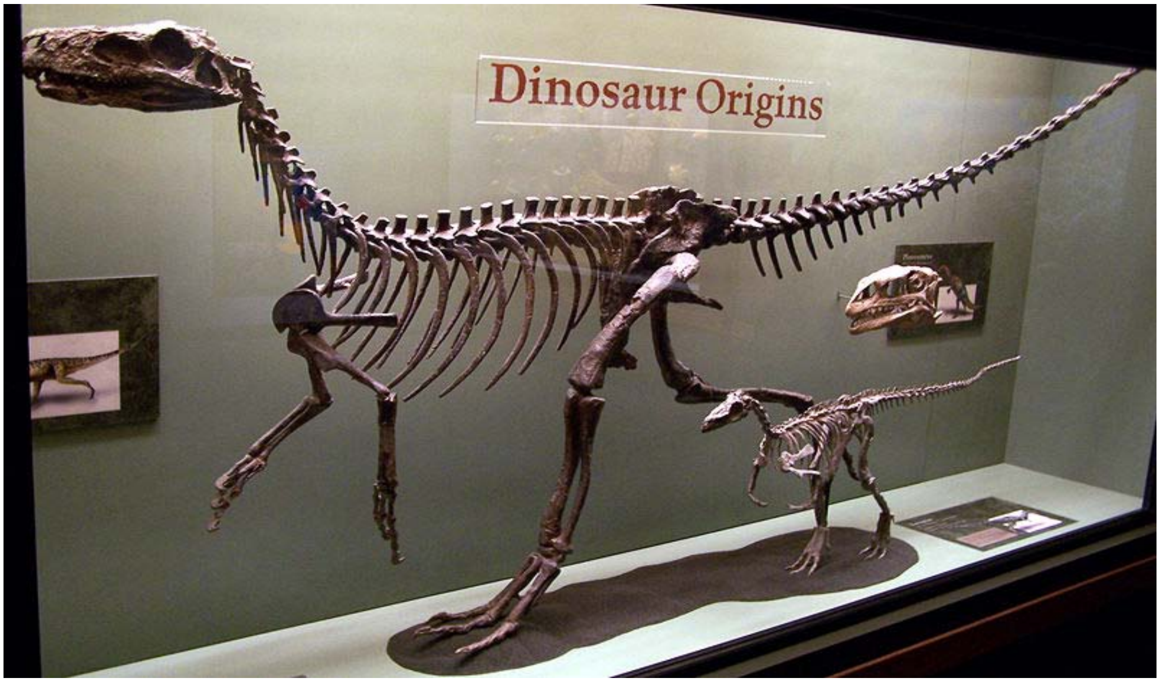


Marasuchus, a dinosaur-like ornithodiran

For a long time many scientists thought dinosaurs were polyphyletic with multiple groups of unrelated "dinosaurs" evolving due to similar pressures, but dinosaurs are now known to have formed a single group.

Dinosaurs diverged from their archosaur ancestors approximately 230 million years ago during the Middle to Late Triassic period, roughly 20 million years after the Permian–Triassic extinction event wiped out an estimated 95% of all life on Earth. Radiometric dating of the rock formation that contained fossils from the early dinosaur genus *Eoraptor* establishes its presence in the fossil record at this time. Paleontologists believe *Eoraptor* resembles the common ancestor of all dinosaurs; if this is true, its traits suggest that the first dinosaurs were small, bipedal predators. The discovery of primitive, dinosaur-like ornithodirans such as *Marasuchus* and *Lagerpeton* in Argentinian Middle Triassic strata supports this view; analysis of recovered fossils suggests that these animals were indeed small, bipedal predators.

When dinosaurs appeared, terrestrial habitats were occupied by various types of basal archosaurs and therapsids, such as aetosaurs, cynodonts, dicynodonts, ornithosuchids, rauisuchias, and rhynchosaurs. Most of these other animals became extinct in the Triassic, in one of two events. First, at about the boundary between the Carnian and Norian faunal stages (about 215 million years ago), dicynodonts and a variety of basal archosauromorphs, including the prolacertiforms and rhynchosaurs, became extinct. This was followed by the Triassic–Jurassic extinction event (about 200 million years ago), that saw the end of most of the other groups of early archosaurs, like aetosaurs, ornithosuchids, phytosaurs, and rauisuchians. These losses left behind a land fauna of crocodylomorphs, dinosaurs, mammals, pterosaurians, and turtles.



The early forms *Herrerasaurus* (large), *Eoraptor* (small) and a *Plateosaurus* skull

The first few lines of primitive dinosaurs diversified through the Carnian and Norian stages of the Triassic, most likely by occupying the niches of groups that became extinct. Traditionally, dinosaurs were thought to have replaced the variety of other Triassic land animals by proving superior through a long period of competition. This now appears unlikely, for several reasons. Dinosaurs do not show a pattern of steadily increasing in diversity and numbers, as would be predicted if they were competitively replacing other groups; instead, they were very rare through the Carnian, making up only 1–2% of individuals present in faunas. In the Norian, however, after the extinction of several other groups, they became significant components of faunas, representing 50–90% of individuals. Also, what had been viewed as a key adaptation of dinosaurs, their erect stance, is now known to have been present in several contemporaneous groups that were not as successful (aetosaurs, ornithosuchids, rauisuchians, and some groups of crocodylomorphs). Finally, the Late Triassic itself was a time of great upheaval in life, with shifts in plant life, marine life, and climate. Crurotarsans, today represented only by crocodilians but in the Late Triassic also encompassing such now-extinct groups as aetosaurs, phytosaurs, ornithosuchians, and rauisuchians, were actually more diverse in the Late Triassic than dinosaurs, indicating that the survival of dinosaurs had more to do with luck than superiority.

Low diversification in the Cretaceous

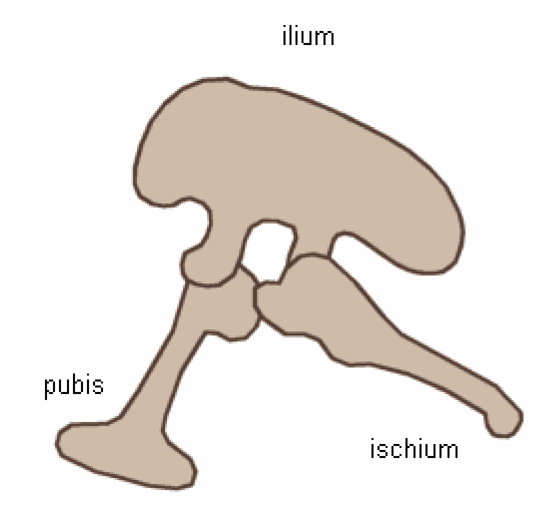
Statistical analyses based on raw data suggest that dinosaurs diversified, i.e. the number of species increased, in the Late Cretaceous. However in July 2008 Graeme T. Lloyd *et al.* argued that this apparent diversification was an illusion caused by sampling bias, because Late Cretaceous rocks have been very heavily studied. Instead, they wrote, dinosaurs underwent only two significant diversifications in the Late Cretaceous, the initial radiations of the euhadrosaurs and ceratopsians. In the Mid Cretaceous, the flowering angiosperm plants became a major part of terrestrial ecosystems, which had previous been dominated by gymnosperms such as conifers. Dinosaur coprolites (fossilized dung) indicate that, while some ate angiosperms, most herbivorous dinosaurs mainly ate gymnosperms. Meanwhile herbivorous insects and mammals diversified rapidly to take advantage of the new type of plant food, while lizards, snakes, crocodilians and birds also diversified at the same time. Lloyd *et al.* suggest that dinosaurs' failure to diversify as ecosystems were changing doomed them to extinction.

Classification

Dinosaurs (including birds) are archosaurs, like modern crocodilians. Archosaurs' diapsid skulls have two holes, called temporal fenestrae, located where the jaw muscles attach, and an additional antorbital fenestra in front of the eyes. Most reptiles (including birds) are diapsids; mammals, with only one temporal fenestra, are called synapsids; and turtles, with no temporal fenestra, are anapsids. Anatomically, dinosaurs share many other archosaur characteristics, including teeth that grow from sockets rather than as direct extensions of the jawbones. Within the archosaur group, dinosaurs are differentiated most noticeably by their gait. Dinosaur legs extend directly beneath the body, whereas the legs of lizards and crocodilians sprawl out to either side.

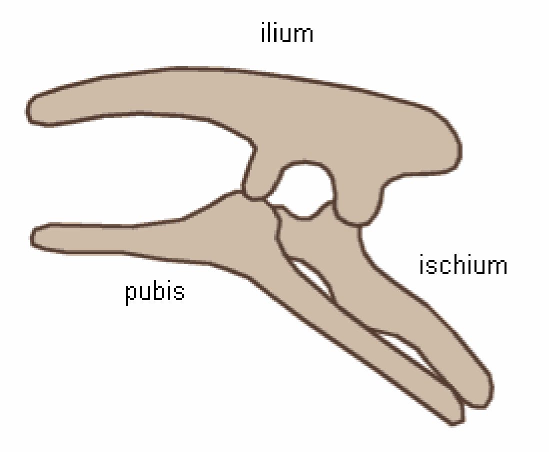
Collectively, dinosaurs are usually regarded as a superorder or an unranked clade. They are divided into two orders, Saurischia and Ornithischia, depending upon pelvic structure. Saurischia includes those taxa sharing a more recent common ancestor with birds than with Ornithischia, while Ornithischia includes all taxa sharing a more recent common ancestor with *Triceratops* than with Saurischia. Saurischians ("lizard-hipped", from the Greek *sauros* (*σαυρος*) meaning "lizard" and *ischion* (*ισχιον*) meaning "hip joint") retained the hip structure of their ancestors, with a pubis bone directed cranially, or forward. This basic form was modified by rotating the pubis backward to varying degrees in several groups (*Herrerasaurus*, therizinosauroids, dromaeosaurids, and birds). Saurischia includes the theropods (bipedal and mostly carnivores, except for birds) and sauropodomorphs (long-necked quadrupedal herbivores).

By contrast, ornithischians ("bird-hipped", from the Greek *ornitheios* (*ορνιθειος*) meaning "of a bird" and *ischion* (*ισχιον*) meaning "hip joint") had a pelvis that superficially resembled a bird's pelvis: the pubis bone was oriented caudally (rear-pointing) Unlike birds, the ornithischian pubis also usually had an additional forward-pointing process. Ornithischia includes a variety of herbivores. (**NB:** the terms "lizard hip" and "bird hip" are misnomers – birds evolved from dinosaurs with "lizard hips".)



Saurischian pelvis structure (left side)

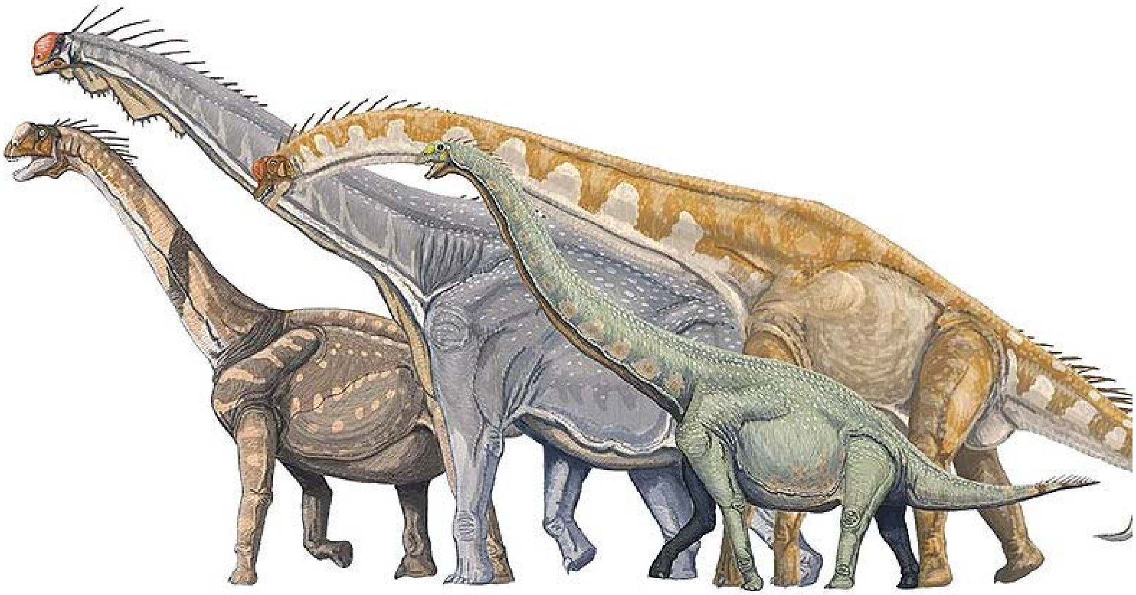
Tyrannosaurus pelvis (showing saurischian structure – left side)



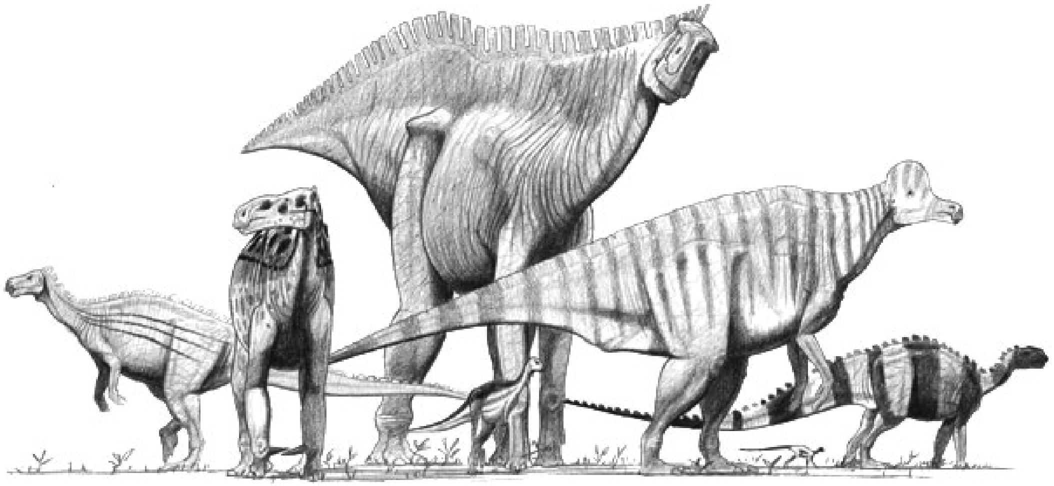
Ornithischian pelvis structure (left side)

Edmontosaurus pelvis (showing ornithischian structure – left side)

The following is a simplified classification of dinosaur families. A more detailed version can be found at List of dinosaur classifications.



Several macronarian Sauropods: from left to right *Camarasaurus*, *Brachiosaurus*, *Giraffatitan*, and *Euhelopus*



Various ornithopod dinosaurs and one heterodontosaurid. Far left: *Camptosaurus*, left: *Iguanodon*, center background: *Shantungosaurus*, center foreground: *Dryosaurus*, right: *Corythosaurus*, far right (small): *Heterodontosaurus*, far right (large) *Tenontosaurus*.

- Dinosauria
    - Saurischia (theropods and sauropods)

- †Herrerasaurians (early bipedal predators)
- Theropods (all bipedal; most were carnivores)

- †Coelophysoids (*Coelophysis* and close relatives)
- †Ceratosaurians (*Ceratosaurus* and abelisaurids – the latter were important Late Cretaceous predators in southern continents)
- †Spinosauroids (long bodies; short arms; some with crocodile-like skulls and bony "sails" on their backs)
- †Carnosaurians (*Allosaurus* and close relatives, like *Carcharodontosaurus*)
- Coelurosaurians (diverse, with a range of body sizes and niches)

- †Tyrannosauroids (small to gigantic, often with reduced forelimbs)
- †Ornithomimosaurians ("ostrich-mimics"; mostly toothless; carnivores to possible herbivores)
- †Therizinosauroids (bipedal herbivores with large hand claws and small heads)
- †Oviraptorosaurians (mostly toothless; their diet and lifestyle are uncertain)
- †Dromaeosaurids (popularly known as "raptors"; bird-like carnivores)
- †Troodontids (similar to dromaeosaurids, but more lightly built)
- Avialans (flying dinosaurs, including modern birds: the only living dinosaurs)

- †Sauropodomorphs (quadrupedal herbivores with small heads, long necks and tails, and elephant-like bodies)

- †"Prosauropods" (early relatives of sauropods; small to quite large; some possibly omnivorous; bipeds and quadrupeds)
- †Sauropods (very large, usually over 15 meters long [49 ft])

- †Diplodocoids (skulls and tails elongated; teeth typically narrow and pencil-like)
- †Macronarians (boxy skulls; spoon-shaped or pencil-shaped teeth)

- †Brachiosaurids (very long necks; forelimbs longer than hindlimbs)
- †Titanosaurians (diverse; stocky, with wide hips; most common in the Late Cretaceous of southern continents)

- †Ornithischians (diverse bipedal and quadrupedal herbivores)

- †Heterodontosaurids (meter- or yard-scale herbivores or omnivores with prominent canine teeth)
- †Thyreophorans (armored dinosaurs; mostly quadrupeds)

- †Ankylosaurians (scutes as primary armor; some had club-like tails)

- †Stegosaurians (spikes and plates as primary armor)
- †Ornithopods (diverse, from meter- or yard-scale bipeds to 12-meter (39 ft) animals that could move as both bipeds and quadrupeds; evolved a method of chewing using skull flexibility and large numbers of teeth)
- †Hadrosaurids ("duckbilled dinosaurs")
- †Pachycephalosaurians ("bone-heads"; bipeds with domed or knobby growth on skulls)
- †Ceratopsians (dinosaurs with horns and frills, although most early forms had only the beginnings of these features)

Evolution and paleobiogeography

Dinosaur evolution after the Triassic follows changes in vegetation and the location of continents. In the Late Triassic and Early Jurassic, the continents were connected as the single landmass Pangaea, and there was a worldwide dinosaur fauna mostly composed of coelophysoid carnivores and prosauropod herbivores. Gymnosperm plants (particularly conifers), a potential food source, radiated in the Late Triassic. Prosauropods did not have sophisticated mechanisms for processing food in the mouth, and so must have employed other means of breaking down food farther along the digestive tract. The general homogeneity of dinosaurian faunas continued into the Middle and Late Jurassic, where most localities had predators consisting of ceratosaurians, spinosauroids, and carnosaurians, and herbivores consisting of stegosaurian ornithischians and large sauropods. Examples of this include the Morrison Formation of North America and Tendaguru Beds of Tanzania. Dinosaurs in China show some differences, with specialized sinraptorid theropods and unusual, long-necked sauropods like *Mamenchisaurus*. Ankylosaurians and ornithopods were also becoming more common, but prosauropods had become extinct. Conifers and pteridophytes were the most common plants. Sauropods, like the earlier prosauropods, were not oral processors, but ornithischians were evolving various means of dealing with food in the mouth, including potential cheek-like organs to keep food in the mouth, and jaw motions to grind food. Another notable evolutionary event of the Jurassic was the appearance of true birds, descended from maniraptoran coelurosaurians.

By the Early Cretaceous and the ongoing breakup of Pangaea, dinosaurs were becoming strongly differentiated by landmass. The earliest part of this time saw the spread of ankylosaurians, iguanodontians, and brachiosaurids through Europe, North America, and northern Africa. These were later supplemented or replaced in Africa by large spinosaurid and carcharodontosaurid theropods, and rebbachisaurid and titanosaurian sauropods, also found in South America. In Asia, maniraptoran coelurosaurians like dromaeosaurids, troodontids, and oviraptorosaurians became the common theropods, and ankylosaurids and early ceratopsians like *Psittacosaurus* became important herbivores. Meanwhile, Australia was home to a fauna of basal ankylosaurians, hypsilophodonts, and iguanodontians. The stegosaurians appear to have gone extinct at some point in the late

Early Cretaceous or early Late Cretaceous. A major change in the Early Cretaceous, which would be amplified in the Late Cretaceous, was the evolution of flowering plants. At the same time, several groups of dinosaurian herbivores evolved more sophisticated ways to orally process food. Ceratopsians developed a method of slicing with teeth stacked on each other in batteries, and iguanodontians refined a method of grinding with tooth batteries, taken to its extreme in hadrosaurids. Some sauropods also evolved tooth batteries, best exemplified by the rebbachisaurid *Nigersaurus*.

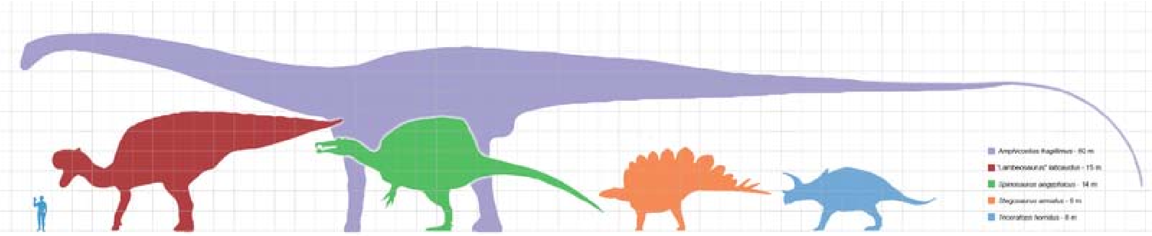
There were three general dinosaur faunas in the Late Cretaceous. In the northern continents of North America and Asia, the major theropods were tyrannosaurids and various types of smaller maniraptoran theropods, with a predominantly ornithischian herbivore assemblage of hadrosaurids, ceratopsians, ankylosaurids, and pachycephalosaurians. In the southern continents that had made up the now-splitting Gondwana, abelisaurids were the common theropods, and titanosaurian sauropods the common herbivores. Finally, in Europe, dromaeosaurids, rhabdodontid iguanodontians, nodosaurid ankylosaurians, and titanosaurian sauropods were prevalent. Flowering plants were greatly radiating, with the first grasses appearing by the end of the Cretaceous. Grinding hadrosaurids and shearing ceratopsians became extremely diverse across North America and Asia. Theropods were also radiating as herbivores or omnivores, with therizinosaurians and ornithomimosaurians becoming common.

The Cretaceous–Tertiary extinction event, which occurred approximately 65 million years ago at the end of the Cretaceous period, caused the extinction of all dinosaurs except for the birds. Some other diapsid groups, such as crocodilians, lizards, snakes, sphenodontians, and choristoderans, also survived the event.

Paleobiology

Knowledge about dinosaurs is derived from a variety of fossil and non-fossil records, including fossilized bones, feces, trackways, gastroliths, feathers, impressions of skin, internal organs and soft tissues. Many fields of study contribute to our understanding of dinosaurs, including physics (especially biomechanics), chemistry, biology, and the earth sciences (of which paleontology is a sub-discipline). Two topics of particular interest and study have been dinosaur size and behavior.

Size



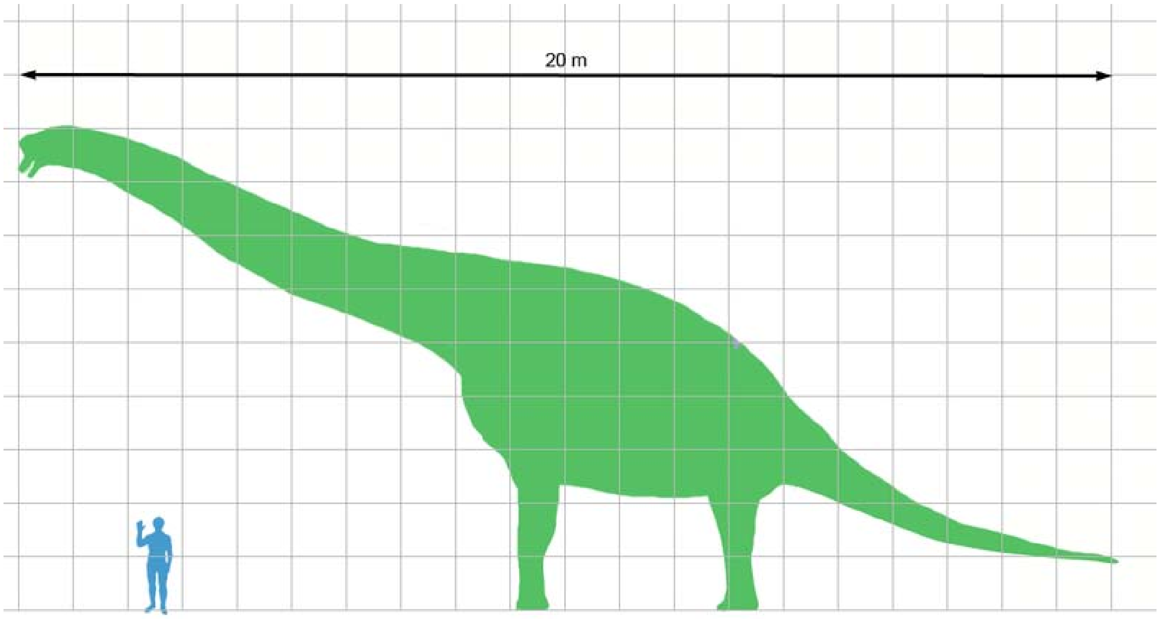
Scale diagram comparing the largest known dinosaurs in five major clades and a human

While the evidence is incomplete, it is clear that, as a group, dinosaurs were large. Even by dinosaur standards, the sauropods were gigantic. For much of the dinosaur era, the smallest sauropods were larger than anything else in their habitat, and the largest were an order of magnitude more massive than anything else that has since walked the Earth. Giant prehistoric mammals such as the *Indricotherium* and the Columbian mammoth were dwarfed by the giant sauropods, and only a handful of modern aquatic animals approach or surpass them in size – most notably the blue whale, which reaches up to 173000 kg (381000 lb) and over 30 meters (100 ft) in length. There are several proposed advantages for the large size of sauropods, including protection from predation, reduction of energy use, and longevity, but it may be that the most important advantage was dietary. Large animals are more efficient at digestion than small animals, because food spends more time in their digestive systems. This also permits them to subsist on food with lower nutritive value than smaller animals. Sauropod remains are mostly found in rock formations interpreted as dry or seasonally dry, and the ability to eat large quantities of low-nutrient browse would have been advantageous in such environments.

Most dinosaurs, however, were much smaller than the giant sauropods. Current evidence suggests that dinosaur average size varied through the Triassic, early Jurassic, late Jurassic and Cretaceous periods. Theropod dinosaurs, when sorted by estimated weight into categories based on order of magnitude, most often fall into the 100 to 1000 kilogram (220 to 2200 lb) category, whereas recent predatory carnivorans peak in the 10 to 100 kilogram (22 to 220 lb) category. The mode of dinosaur body masses is between one and ten metric tonnes. This contrasts sharply with the size of Cenozoic mammals, estimated by the National Museum of Natural History as about 2 to 5 kilograms (5 to 10 lb).

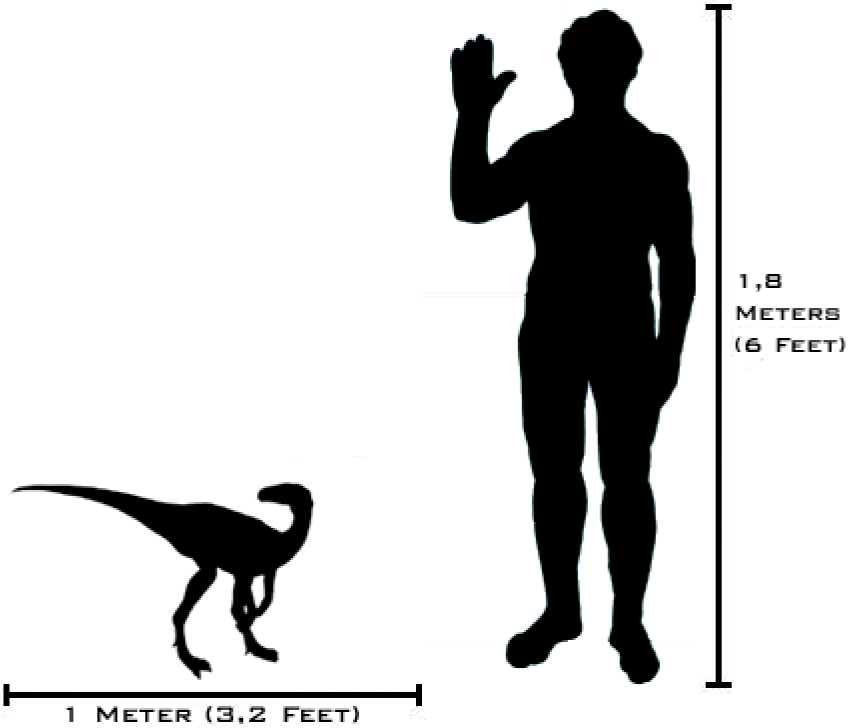
Largest and smallest

Only a tiny percentage of animals ever fossilize, and most of these remain buried in the earth. Few of the specimens that are recovered are complete skeletons, and impressions of skin and other soft tissues are rare. Rebuilding a complete skeleton by comparing the size and morphology of bones to those of similar, better-known species is an inexact art, and reconstructing the muscles and other organs of the living animal is, at best, a process of educated guesswork. As a result, scientists will probably never be certain of the largest and smallest dinosaurs.



Comparative size of *Giraffatitan*

The tallest and heaviest dinosaur known from good skeletons is *Giraffatitan brancai* (previously classified as a species of *Brachiosaurus*). Its remains were discovered in Tanzania between 1907–12. Bones from multiple similar-sized individuals were incorporated into the skeleton now mounted and on display at the Humboldt Museum of Berlin; this mount is 12 meters (39 ft) tall and 22.5 meters (74 ft) long, and would have belonged to an animal that weighed between 30000 and 60000 kilograms (70000 and 130000 lb). The longest complete dinosaur is the 27-meter (89 ft) long *Diplodocus*, which was discovered in Wyoming in the United States and displayed in Pittsburgh's Carnegie Natural History Museum in 1907.



Comparative size of *Eoraptor*

There were larger dinosaurs, but knowledge of them is based entirely on a small number of fragmentary fossils. Most of the largest herbivorous specimens on record were all discovered in the 1970s or later, and include the massive *Argentinosaurus*, which may have weighed 80000 to 100000 kilograms (90 to 110 short tons); some of the longest were the 33.5 meters (110 ft) long *Diplodocus hallorum* (formerly *Seismosaurus*) and the 33 meters (110 ft) long *Supersaurus*; and the tallest, the 18 meters (59 ft) tall *Sauroposeidon*, which could have reached a sixth-floor window. The longest of them all may have been *Amphicoelias fragillimus*, known only from a now lost partial vertebral neural arch described in 1878. Extrapolating from the illustration of this bone, the animal may have been 58 meters (190 ft) long and weighed over 120000 kg (260000 lb). The largest known carnivorous dinosaur was *Spinosaurus*, reaching a length of 16 to 18 meters (50 to 60 ft), and weighing in at 8150 kg (18000 lb). Other large meat-eaters included *Giganotosaurus*, *Carcharodontosaurus* and *Tyrannosaurus*.

Not including modern birds, the smallest dinosaurs known were about the size of a pigeon. The theropods *Anchiornis* and *Epidexipteryx* both had a total skeletal length of under 35 centimeters (1.1 ft). *Anchiornis* is currently the smallest dinosaur described from an adult specimen, with an estimated weight of 110 grams. The smallest herbivorous dinosaurs included *Microceratus* and *Wannanosaurus*, at about 60 cm (2 ft) long each.

Behavior

A nesting ground of *Maiasaura* was discovered in 1978

Interpretations of dinosaur behavior are generally based on the pose of body fossils and their habitat, computer simulations of their biomechanics, and comparisons with modern animals in similar ecological niches. As such, the current understanding of dinosaur behavior relies on speculation, and will likely remain controversial for the foreseeable future. However, there is general agreement that some behaviors which are common in crocodiles and birds, dinosaurs' closest living relatives, were also common among dinosaurs.

The first potential evidence of herding behavior was the 1878 discovery of 31 *Iguanodon* dinosaurs which were then thought to have perished together in Bernissart, Belgium, after they fell into a deep, flooded sinkhole and drowned. Other mass-death sites have been subsequently discovered. Those, along with multiple trackways, suggest that gregarious behavior was common in many dinosaur species. Trackways of hundreds or even thousands of herbivores indicate that duck-bills (hadrosaurids) may have moved in great herds, like the American Bison or the African Springbok. Sauropod tracks document that these animals traveled in groups composed of several different species, at least in Oxfordshire, England, although there is not evidence for specific herd structures. Dinosaurs may have congregated in herds for defense, for migratory purposes, or to provide protection for their young. There is evidence that many types of dinosaurs, including various theropods, sauropods, ankylosaurians, ornithopods, and ceratopsians, formed aggregations of immature individuals. One example is a site in Inner Mongolia that has yielded the remains of over twenty *Sinornithomimus*, from one to seven years old. This assemblage is interpreted as a social group that was trapped in mud. The interpretation of dinosaurs as gregarious has also extended to depicting carnivorous theropods as pack hunters working together to bring down large prey. However, this lifestyle is uncommon among the modern relatives of dinosaurs (crocodiles and other reptiles, and birds – Harris's Hawk is a well-documented exception), and the taphonomic evidence suggesting pack hunting in such theropods as *Deinonychus* and *Allosaurus* can also be interpreted as the results of fatal disputes between feeding animals, as is seen in many modern diapsid predators.

Fossilized egg of the oviraptorid *Citipati*, American Museum of Natural History

Jack Horner's 1978 discovery of a *Maiasaura* ("good mother dinosaur") nesting ground in Montana demonstrated that parental care continued long after birth among the ornithopods. There is also evidence that other Cretaceous-era dinosaurs, like Patagonian titanosaurian sauropods (1997 discovery), also nested in large groups. The Mongolian oviraptorid *Citipati* was discovered in a chicken-like brooding position in 1993, which may mean it was covered with an insulating layer of feathers that kept the eggs warm. Parental care is also implied by other finds. For example, the fossilized remains of a grouping of *Psittacosaurus* has been found, consisting of one adult and 34 juveniles; in this case, the large number of juveniles may be due to communal nesting. Additionally, a dinosaur embryo (pertaining to the prosauropod *Massospondylus*) was found without teeth, indicating that some parental care was required to feed the young dinosaur. Trackways have also confirmed parental behavior among ornithopods from the Isle of Skye in northwestern Scotland. Nests and eggs have been found for most major groups of dinosaurs, and it appears likely that dinosaurs communicated with their young, in a manner similar to modern birds and crocodiles.

Artist's rendering of two *Centrosaurus*, herbivorous ceratopsid dinosaurs from the late Cretaceous fauna of North America

The crests and frills of some dinosaurs, like the marginocephalians, theropods and lambeosaurines, may have been too fragile to be used for active defense, and so they were likely used for sexual or aggressive displays, though little is known about dinosaur mating and territorialism. Head wounds from bites suggest that theropods, at least, engaged in active aggressive confrontations.

From a behavioral standpoint, one of the most valuable dinosaur fossils was discovered in the Gobi Desert in 1971. It included a *Velociraptor* attacking a *Protoceratops*, providing evidence that dinosaurs did indeed attack each other. Additional evidence for attacking live prey is the partially healed tail of an *Edmontosaurus*, a hadrosaurid dinosaur; the tail is damaged in such a way that shows the animal was bitten by a tyrannosaur but survived. Cannibalism amongst some species of dinosaurs was confirmed by tooth marks found in Madagascar in 2003, involving the theropod *Majungasaurus*.

Based on current fossil evidence from dinosaurs such as *Oryctodromeus*, some herbivorous species seem to have led a partially fossorial (burrowing) lifestyle, and some bird-like species may have been arboreal (tree-climbing), most notably primitive dromaeosaurids such as *Microraptor* and the enigmatic scansoriopterygids. However, most dinosaurs seem to have relied on land-based locomotion. A good understanding of how dinosaurs moved on the ground is key to models of dinosaur behavior; the science of biomechanics, in particular, has provided significant insight in this area. For example, studies of the forces exerted by muscles and gravity on dinosaurs' skeletal structure have investigated how fast dinosaurs could run, whether diplodocids could create sonic booms via whip-like tail snapping, and whether sauropods could float.

Communication and vocalization

The nature of dinosaur communication remains enigmatic, and is an active area of research. In 2008, paleontologist Phil Senter examined the evidence for vocalization in Mesozoic animal life, including dinosaurs. Senter found that, contrary to popular depictions of roaring dinosaurs in motion pictures, it is likely that most dinosaurs were not capable of creating any vocalizations. To draw this conclusion, Senter studied the distribution of vocal organs in reptiles and birds. He found that vocal chords in the larynx probably evolved multiple times among reptiles, including crocodilians, which are able to produce guttural roars. Birds, on the other hand, lack a larynx. Instead, bird calls are produced by the syrinx, a vocal organ found only in birds, and which is not related to the larynx, meaning it evolved independently from the vocal organs in reptiles. The syrinx depends on the air sac system in birds to function; specifically, it requires the presence of a *clavicular air sac* near the wishbone or collar bone. This air sac leaves distinctive marks or opening on the bones, including a distinct opening in the upper arm bone (*humerus*). While many dinosaurs show evidence of extensive air sac systems, almost none possess the clavicular air sac necessary to vocalize (one exception, *Aerosteon*, probably evolved its clavicular air sac independently of birds for reasons other than vocalization).

The most primitive animals with evidence of a vocalizing syrinx are the enantironithine birds. Any bird-line archosaurs more primitive than this probably did not make vocal calls. Rather, several lines of evidence suggest that dinosaurs used primarily visual communication, in the form of distinctive-looking (and possibly brightly colored) horns, frills, crests, sails and feathers. This is similar to some modern reptile groups such as lizards, in which many forms are largely silent (though like dinosaurs they possess well-developed senses of hearing) but use complex coloration and display behaviors to communicate.

Also, though they may not have been able to vocalize, some dinosaurs may have used other methods of producing sound for communication. Modern animals, including reptiles and birds, use a wide variety of non-vocal sound communication, including hissing, jaw grinding or clapping, use of environment (such as splashing), and wing beating (which would have been possible in winged maniraptoran dinosaurs).

Some studies have suggested that the hollow crests of the lambeosaurines may have functioned as resonance chambers used for a wide range of vocalizations. However, Senter (2008) noted that such chambers are also used in modern non-vocal animals to accentuate or deepen non-vocal sounds like hissing. For example, many snakes, which lack vocal chords, have resonating chambers in the skull.

Physiology

Tyrannosaurus rex skull and upper vertebral column, Palais de la Découverte, Paris

A vigorous debate on the subject of temperature regulation in dinosaurs has been ongoing since the 1960s. Originally, scientists broadly disagreed as to whether dinosaurs were capable of regulating their body temperatures at all. More recently, dinosaur endothermy has become the consensus view, and debate has focused on the mechanisms of temperature regulation.

After dinosaurs were discovered, paleontologists first posited that they were ectothermic creatures: "terrible lizards" as their name suggests. This supposed cold-bloodedness implied that dinosaurs were relatively slow, sluggish organisms, comparable to modern reptiles, which need external sources of heat in order to regulate their body temperature. Dinosaur ectothermy remained a prevalent view until Robert T. "Bob" Bakker, an early proponent of dinosaur endothermy, published an influential paper on the topic in 1968.

Modern evidence indicates that dinosaurs thrived in cooler temperate climates, and that at least some dinosaur species must have regulated their body temperature by internal biological means (perhaps aided by the animals' bulk). Evidence of endothermy in dinosaurs includes the discovery of polar dinosaurs in Australia and Antarctica (where they would have experienced a cold, dark six-month winter), the discovery of dinosaurs whose feathers may have provided regulatory insulation, and analysis of blood-vessel structures within dinosaur bone that are typical of endotherms. Skeletal structures suggest that theropods and other dinosaurs had active lifestyles better suited to an endothermic cardiovascular system, while sauropods exhibit fewer endothermic characteristics. It is certainly possible that some dinosaurs were endothermic while others were not. Scientific debate over the specifics continues.

Eubrontes, a dinosaur footprint in the Lower Jurassic Moenave Formation at the St. George Dinosaur Discovery Site at Johnson Farm, southwestern Utah

Complicating the debate is the fact that warm-bloodedness can emerge based on more than one mechanism. Most discussions of dinosaur endothermy tend to compare them with average-sized birds or mammals, which expend energy to elevate body temperature above that of the environment. Small birds and mammals also possess insulation, such as fat, fur, or feathers, which slows down heat loss. However, large mammals, such as elephants, face a different problem because of their relatively small ratio of surface area to volume (Haldane's principle). This ratio compares the volume of an animal with the area of its skin: as an animal gets bigger, its surface area increases more slowly than its volume. At a certain point, the amount of heat radiated away through the skin drops below the amount of heat produced inside the body, forcing animals to use additional methods to avoid overheating. In the case of elephants, they have little hair as adults, have large ears which increase their surface area, and have behavioral adaptations as well (such as using the trunk to spray water on themselves and mud-wallowing). These behaviors increase cooling through evaporation.

Large dinosaurs would presumably have had to deal with similar issues; their body size suggest they lost heat relatively slowly to the surrounding air, and so could have been what are called inertial homeotherms, animals that are warmer than their environments through sheer size rather than through special adaptations like those of birds or mammals. However, so far this theory fails to account for the numerous dog- and goat-sized dinosaur species, or the young of larger species.

Modern computerized tomography (CT) scans of a dinosaur's chest cavity (conducted in 2000) found the apparent remnants of a four-chambered heart, much like those found in today's mammals and birds. The idea is controversial within the scientific community, coming under fire for bad anatomical science or simply wishful thinking. The question of how this find reflects on metabolic rate and dinosaur internal anatomy may be moot, though, regardless of the object's identity: both modern crocodilians and birds, the closest living relatives of dinosaurs, have four-chambered hearts (albeit modified in crocodilians), and so dinosaurs probably had them as well.

Soft tissue and DNA

One of the best examples of soft-tissue impressions in a fossil dinosaur was discovered in Petraroia, Italy. The discovery was reported in 1998, and described the specimen of a small, very young coelurosaur, *Scipionyx samniticus*. The fossil includes portions of the intestines, colon, liver, muscles, and windpipe of this immature dinosaur.

In the March 2005 issue of *Science*, the paleontologist Mary Higby Schweitzer and her team announced the discovery of flexible material resembling actual soft tissue inside a 68-million-year-old *Tyrannosaurus rex* leg bone from the Hell Creek Formation in Montana. After recovery, the tissue was rehydrated by the science team.

When the fossilized bone was treated over several weeks to remove mineral content from the fossilized bone-marrow cavity (a process called demineralization), Schweitzer found evidence of intact structures such as blood vessels, bone matrix, and connective tissue (bone fibers). Scrutiny under the microscope further revealed that the putative dinosaur soft tissue had retained fine structures (microstructures) even at the cellular level. The exact nature and composition of this material, and the implications of Schweitzer's discovery, are not yet clear; study and interpretation of the material is ongoing.

Newer research, published in PloS One (30 July 2008), has challenged the claims that the material found is the soft tissue of *Tyrannosaurus*. Thomas Kaye of the University of

Washington and his co-authors contend that what was really inside the tyrannosaur bone was slimy biofilm created by bacteria that coated the voids once occupied by blood vessels and cells. The researchers found that what previously had been identified as remnants of blood cells, because of the presence of iron, were actually framboids, microscopic mineral spheres bearing iron. They found similar spheres in a variety of other fossils from various periods, including an ammonite. In the ammonite they found the spheres in a place where the iron they contain could not have had any relationship to the presence of blood.

The successful extraction of ancient DNA from dinosaur fossils has been reported on two separate occasions, but, upon further inspection and peer review, neither of these reports could be confirmed. However, a functional visual peptide of a theoretical dinosaur has been inferred using analytical phylogenetic reconstruction methods on gene sequences of related modern species such as reptiles and birds. In addition, several proteins, including hemoglobin, have putatively been detected in dinosaur fossils.

Feathers and the origin of birds

The possibility that dinosaurs were the ancestors of birds was first suggested in 1868 by Thomas Henry Huxley. After the work of Gerhard Heilmann in the early 20th century, the theory of birds as dinosaur descendants was abandoned in favor of the idea of their being descendants of generalized thecodonts, with the key piece of evidence being the supposed lack of clavicles in dinosaurs. However, as later discoveries showed, clavicles (or a single fused wishbone, which derived from separate clavicles) were not actually absent; they had been found as early as 1924 in *Oviraptor*, but misidentified as an interclavicle. In the 1970s, John Ostrom revived the dinosaur–bird theory, which gained momentum in the coming decades with the advent of cladistic analysis, and a great increase in the discovery of small theropods and early birds. Of particular note have been the fossils of the Yixian Formation, where a variety of theropods and early birds have been found, often with feathers of some type. Birds share over a hundred distinct anatomical features with theropod dinosaurs, which are now generally accepted to have been their closest ancient relatives. They are most closely allied with maniraptoran coelurosaurs. A minority of scientists, most notably Alan Feduccia and Larry Martin, have proposed other evolutionary paths, including revised versions of Heilmann's basal archosaur proposal, or that maniraptoran theropods are the ancestors of birds but themselves are not dinosaurs, only convergent with dinosaurs.

Feathers

The famous Berlin Specimen of *Archaeopteryx lithographica*

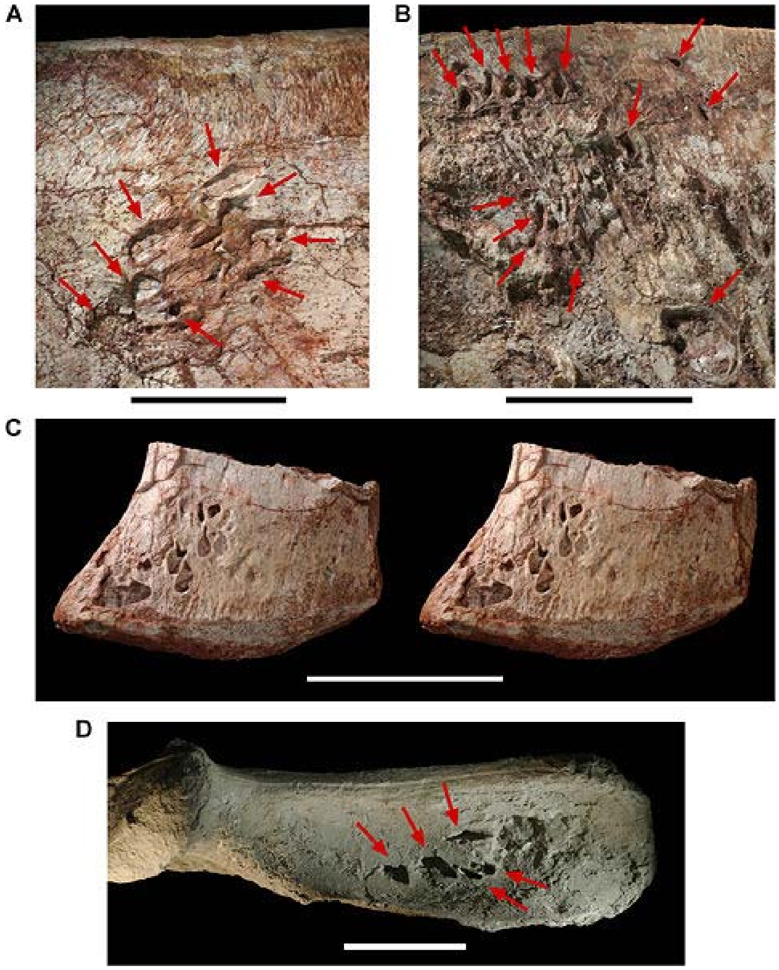
Archaeopteryx, the first good example of a "feathered dinosaur", was discovered in 1861. The initial specimen was found in the Solnhofen limestone in southern Germany, which is a *lagerstätte*, a rare and remarkable geological formation known for its superbly detailed fossils. *Archaeopteryx* is a transitional fossil, with features clearly intermediate between those of modern reptiles and birds. Brought to light just two years after Darwin's seminal *The Origin of Species*, its discovery spurred the nascent debate between proponents of evolutionary biology and creationism. This early bird is so dinosaur-like that, without a clear impression of feathers in the surrounding rock, at least one specimen was mistaken for *Compsognathus*.

Since the 1990s, a number of additional feathered dinosaurs have been found, providing even stronger evidence of the close relationship between dinosaurs and modern birds. Most of these specimens were unearthed in the lagerstätte of the Yixian Formation, Liaoning, northeastern China, which was part of an island continent during the Cretaceous. Though feathers have been found in only a few locations, it is possible that non-avian dinosaurs elsewhere in the world were also feathered. The lack of widespread fossil evidence for feathered non-avian dinosaurs may be because delicate features like skin and feathers are not often preserved by fossilization and thus are absent from the fossil record. To this point, protofeathers (thin, filament-like structures) are known from dinosaurs at the base of Coelurosauria, such as compsognathids like *Sinosauropteryx* and tyrannosauroids (*Dilong*), but barbed feathers are known only among the coelurosaur subgroup Maniraptora, which includes oviraptorosaurs, troodontids, dromaeosaurids, and birds. The description of feathered dinosaurs has not been without controversy; perhaps the most vocal critics have been Alan Feduccia and Theagarten Lingham-Soliar, who have proposed that protofeathers are the result of the decomposition of collagenous fiber that underlaid the dinosaurs' integument, and that maniraptoran dinosaurs with barbed feathers were not actually dinosaurs, but convergent with dinosaurs. However, their views have for the most part not been accepted by other researchers, to the point that the question of the scientific nature of Feduccia's proposals has been raised.

Skeleton

Because feathers are often associated with birds, feathered dinosaurs are often touted as the missing link between birds and dinosaurs. However, the multiple skeletal features also shared by the two groups represent another important line of evidence for paleontologists. Areas of the skeleton with important similarities include the neck, pubis, wrist (semi-lunate carpal), arm and pectoral girdle, furcula (wishbone), and breast bone. Comparison of bird and dinosaur skeletons through cladistic analysis strengthens the case for the link.

Soft anatomy



Pneumatopores on the left ilium of *Aerosteon riocoloradensis*

Large meat-eating dinosaurs had a complex system of air sacs similar to those found in modern birds, according to an investigation which was led by Patrick O'Connor of Ohio University. The lungs of theropod dinosaurs (carnivores that walked on two legs and had bird-like feet) likely pumped air into hollow sacs in their skeletons, as is the case in birds. "What was once formally considered unique to birds was present in some form in the ancestors of birds", O'Connor said. In a 2008 paper published in the online journal *PLoS ONE*, scientists described *Aerosteon riocoloradensis*, the skeleton of which supplies the strongest evidence to date of a dinosaur with a bird-like breathing system. CT-scanning revealed the evidence of air sacs within the body cavity of the *Aerosteon* skeleton.

Another piece of evidence that birds and dinosaurs are closely related is the use by both of gizzard stones. These stones are swallowed by animals to aid digestion and break down food and hard fibers once they enter the stomach. When found in association with fossils, gizzard stones are called gastroliths.

Reproductive biology

A discovery of features in a *Tyrannosaurus rex* skeleton recently provided more evidence that dinosaurs and birds evolved from a common ancestor and, for the first time, allowed paleontologists to establish the sex of a dinosaur. When laying eggs, female birds grow a special type of bone between the hard outer bone and the marrow of their limbs. This *medullary* bone, which is rich in calcium, is used to make eggshells. The presence of endosteally derived bone tissues lining the interior marrow cavities of portions of the *Tyrannosaurus rex* specimen's hind limb suggested that *T. rex* used similar reproductive strategies, and revealed the specimen to be female. Further research has found medullary bone in the theropod *Allosaurus* and the ornithopod *Tenontosaurus*. Because the line of dinosaurs that includes *Allosaurus* and *Tyrannosaurus* diverged from the line that led to *Tenontosaurus* very early in the evolution of dinosaurs, this suggests that dinosaurs in general produced medullary tissue. Medullary bone has been found in specimens of sub-adult size, which suggests that dinosaurs reached sexual maturity rather quickly for such large animals.

Behavioral evidence

A recently discovered troodont fossil demonstrates that some dinosaurs slept with their heads tucked under their arms. This behavior, which may have helped to keep the head warm, is also characteristic of modern birds.

Extinction

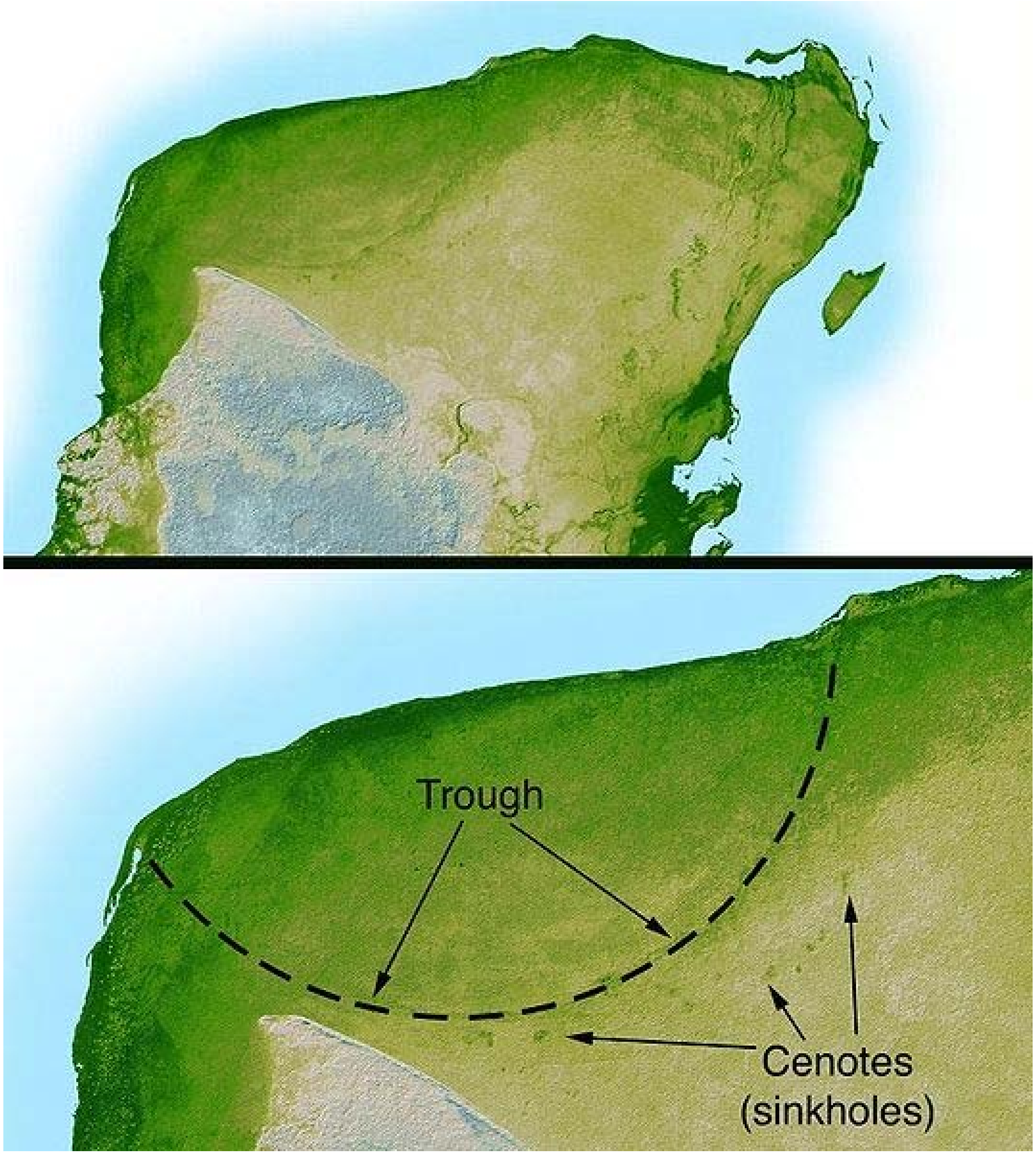
Non-avian dinosaurs suddenly became extinct approximately 65 million years ago. Many other groups of animals also became extinct at this time, including ammonites (nautilus-like mollusks), mosasaurs, plesiosaurs, pterosaurs, most birds, and many groups of mammals. This mass extinction is known as the Cretaceous–Tertiary extinction event. The nature of the event that caused this mass extinction has been extensively studied since the 1970s; at present, several related theories are supported by paleontologists.

Though the consensus is that an impact event was the primary cause of dinosaur extinction, some scientists cite other possible causes, or support the idea that a confluence of several factors was responsible for the sudden disappearance of dinosaurs from the fossil record.

At the peak of the Mesozoic, there were no polar ice caps, and sea levels are estimated to have been from 100 to 250 meters (300 to 800 ft) higher than they are today. The planet's temperature was also much more uniform, with only 25 °C (45 °F) separating average polar temperatures from those at the equator. On average, atmospheric temperatures were also much higher; the poles, for example, were 50 °C (90 °F) warmer than today.

The atmosphere's composition during the Mesozoic was vastly different as well. Carbon dioxide levels were up to 12 times higher than today's levels, and oxygen formed 32 to 35% of the atmosphere, as compared to 21% today. However, by the late Cretaceous, the environment was changing dramatically. Volcanic activity was decreasing, which led to a cooling trend as levels of atmospheric carbon dioxide dropped. Oxygen levels in the atmosphere also started to fluctuate and would ultimately fall considerably. Some scientists hypothesize that climate change, combined with lower oxygen levels, might have led directly to the demise of many species. If the dinosaurs had respiratory systems similar to those commonly found in modern birds, it may have been particularly difficult for them to cope with reduced respiratory efficiency, given the enormous oxygen demands of their very large bodies.

Impact event



The Chicxulub Crater at the tip of the Yucatán Peninsula; the impactor that formed this crater may have caused the dinosaur extinction.

The asteroid collision theory, which was brought to wide attention in 1980 by Walter Alvarez and colleagues, links the extinction event at the end of the Cretaceous period to a bolide impact approximately 65.5 million years ago. Alvarez *et al.* proposed that a sudden increase in iridium levels, recorded around the world in the period's rock stratum, was direct evidence of the impact. The bulk of the evidence now suggests that a bolide 5 to 15 kilometers (3 to 9 mi) wide hit in the vicinity of the Yucatán Peninsula, creating the approximately 180 km (110 mi) Chicxulub Crater and triggering the mass extinction. Scientists are not certain whether dinosaurs were thriving or declining before the impact event. Some scientists propose that the meteorite caused a long and unnatural drop in Earth's atmospheric temperature, while others claim that it would have instead created an unusual heat wave.

Although the speed of extinction cannot be deduced from the fossil record alone, various models suggest that the extinction was extremely rapid. The consensus among scientists who support this theory is that the impact caused extinctions both directly (by heat from the meteorite impact) and also indirectly (via a worldwide cooling brought about when matter ejected from the impact crater reflected thermal radiation from the sun).

In September 2007, U.S. researchers led by William Bottke of the Southwest Research Institute in Boulder, Colorado, and Czech scientists used computer simulations to identify the probable source of the Chicxulub impact. They calculated a 90% probability that a giant asteroid named Baptistina, approximately 160 km (100 mi) in diameter, orbiting in the asteroid belt which lies between Mars and Jupiter, was struck by a smaller unnamed asteroid about 55 km (35 mi) in diameter about 160 million years ago. The impact shattered Baptistina, creating a cluster which still exists today as the Baptistina family. Calculations indicate that some of the fragments were sent hurtling into earth-crossing orbits, one of which was the 10 km (6 mi) wide meteorite which struck Mexico's Yucatan peninsula 65 million years ago, creating the Chicxulub crater.

A similar but more controversial explanation proposes that "passages of the [hypothetical] solar companion star Nemesis through the Oort comet cloud would trigger comet showers." One or more of these comets then collided with the Earth at approximately the same time, causing the worldwide extinction. As with the impact of a single asteroid, the end result of this comet bombardment would have been a sudden drop in global temperatures, followed by a protracted cool period.

Deccan Traps

Before 2000, arguments that the Deccan Traps flood basalts caused the extinction were usually linked to the view that the extinction was gradual, as the flood basalt events were thought to have started around 68 million years ago and lasted for over 2 million years. However, there is evidence that two-thirds of the Deccan Traps were created in only 1 million years about 65.5 million years ago, and so these eruptions would have caused a fairly rapid extinction, possibly over a period of thousands of years, but still longer than would be expected from a single impact event.

The Deccan Traps could have caused extinction through several mechanisms, including the release into the air of dust and sulphuric aerosols, which might have blocked sunlight and thereby reduced photosynthesis in plants. In addition, Deccan Trap volcanism might have resulted in carbon dioxide emissions, which would have increased the greenhouse effect when the dust and aerosols cleared from the atmosphere. Before the mass extinction of the dinosaurs, the release of volcanic gases during the formation of the Deccan Traps "contributed to an apparently massive global warming. Some data point to an average rise in temperature of 8 °C (14 °F) in the last half million years before the impact [at Chicxulub]."

In the years when the Deccan Traps theory was linked to a slower extinction, Luis Alvarez (who died in 1988) replied that paleontologists were being misled by sparse data. While his assertion was not initially well-received, later intensive field studies of fossil beds lent weight to his claim. Eventually, most paleontologists began to accept the idea that the mass extinctions at the end of the Cretaceous were largely or at least partly due to a massive Earth impact. However, even Walter Alvarez has acknowledged that there were other major changes on Earth even before the impact, such as a drop in sea level and massive volcanic eruptions that produced the Indian Deccan Traps, and these may have contributed to the extinctions.

Failure to adapt to changing conditions

Lloyd *et al.* (2008) noted that, in the Mid Cretaceous, the flowering, angiosperm plants became a major part of terrestrial ecosystems, which had previously been dominated by gymnosperms such as conifers. Dinosaur coprolite–fossilized dung–indicate that, while some ate angiosperms, most herbivorous dinosaurs ate mainly gymnosperms. Statistical analysis by Lloyd *et al.* concluded that, contrary to earlier studies, dinosaurs did not diversify very much in the Late Cretaceous. Lloyd *et al.* suggested that dinosaurs' failure to diversify as ecosystems were changing doomed them to extinction.

Possible Paleocene survivors

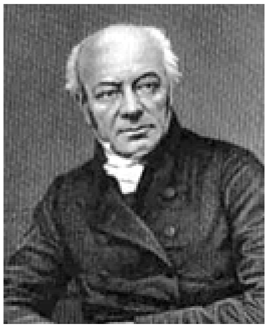
Non-avian dinosaur remains are occasionally found above the K–T boundary. In 2001, paleontologists Zielinski and Budahn reported the discovery of a single hadrosaur leg-bone fossil in the San Juan Basin, New Mexico, and described it as evidence of Paleocene dinosaurs. The formation in which the bone was discovered has been dated to the early Paleocene epoch, approximately 64.5 million years ago. If the bone was not re-deposited into that stratum by weathering action, it would provide evidence that some dinosaur populations may have survived at least a half million years into the Cenozoic Era. Other evidence includes the finding of dinosaur remains in the Hell Creek Formation up to 1.3 meters (51 in) above (40000 years later than) the K–T boundary. Similar reports have come from other parts of the world, including China. Many scientists, however, dismissed the supposed Paleocene dinosaurs as re-worked, i.e. washed out of their original locations and then re-buried in much later sediments. However, direct dating of the bones themselves has supported the later date, with U-Pb dating methods resulting in a precise age of 64.8 ± 0.9 million years ago. If correct, the presence of a handful of dinosaurs in the early Paleocene would not change the underlying facts of the extinction.

History of discovery

Dinosaur fossils have been known for millennia, although their true nature was not recognized. The Chinese, whose modern word for dinosaur is *konglong* (恐龍, or "terrible dragon"), considered them to be dragon bones and documented them as such.

For example, *Hua Yang Guo Zhi*, a book written by Zhang Qu during the Western Jin Dynasty, reported the discovery of dragon bones at Wucheng in Sichuan Province. Villagers in central China have long unearthed fossilized "dragon bones" for use in traditional medicines, a practice that continues today. In Europe, dinosaur fossils were generally believed to be the remains of giants and other creatures killed by the Great Flood.

Scholarly descriptions of what would now be recognized as dinosaur bones first appeared in the late 17th century in England. Part of a bone, now known to have been the femur of a *Megalosaurus*, was recovered from a limestone quarry at Cornwell near Chipping Norton, Oxfordshire, England, in 1676. The fragment was sent to Robert Plot, Professor of Chemistry at the University of Oxford and first curator of the Ashmolean Museum, who published a description in his *Natural History of Oxfordshire* in 1677. He correctly identified the bone as the lower extremity of the femur of a large animal, and recognized that it was too large to belong to any known species. He therefore concluded it to be the thigh bone of a giant human similar to those mentioned in the Bible. In 1699, Edward Lhuyd, a friend of Sir Isaac Newton, was responsible for the first published scientific treatment of what would now be recognized as a dinosaur when he described and named a sauropod tooth, "Rutellum implicatum", that had been found in Caswell, near Witney, Oxfordshire.



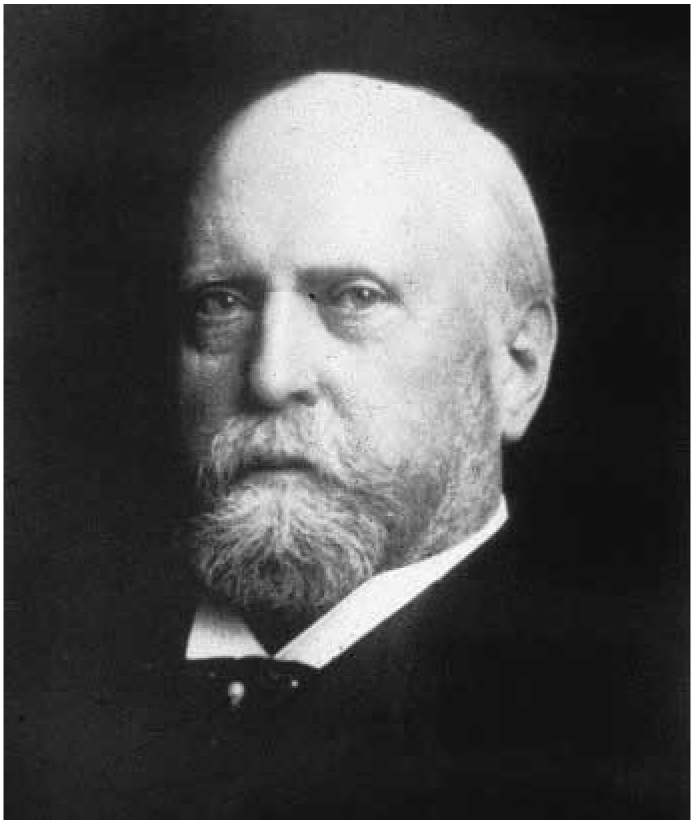
William Buckland

Between 1815 and 1824, the Rev William Buckland, a professor of geology at Oxford University, collected more fossilized bones of *Megalosaurus* and became the first person to describe a dinosaur in a scientific journal. The second dinosaur genus to be identified, *Iguanodon*, was discovered in 1822 by Mary Ann Mantell – the wife of English geologist Gideon Mantell. Gideon Mantell recognized similarities between his fossils and the bones of modern iguanas. He published his findings in 1825.

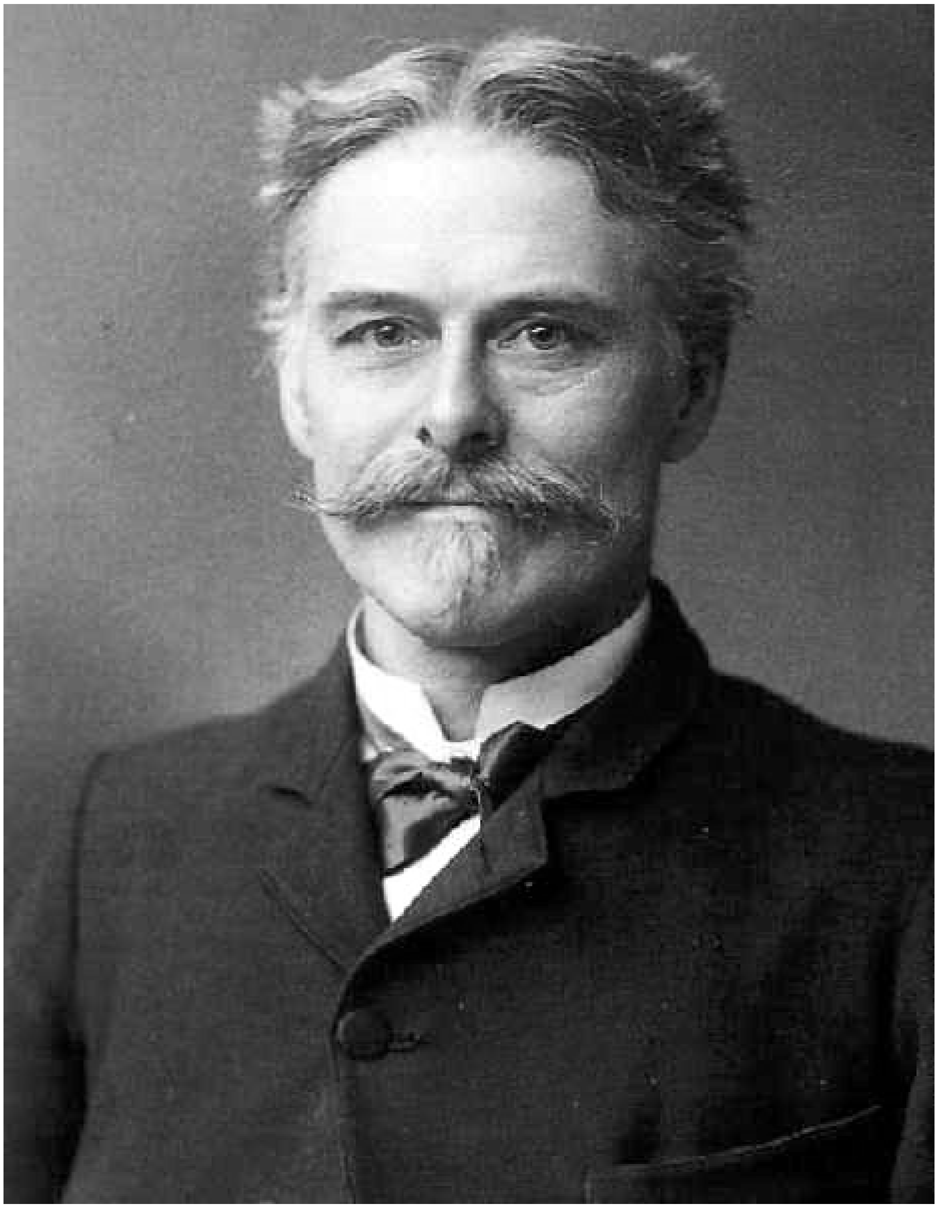
The study of these "great fossil lizards" soon became of great interest to European and American scientists, and in 1842 the English paleontologist Richard Owen coined the term "dinosaur". He recognized that the remains that had been found so far, *Iguanodon*, *Megalosaurus* and *Hylaeosaurus*, shared a number of distinctive features, and so decided to present them as a distinct taxonomic group. With the backing of Prince Albert of Saxe-Coburg-Gotha, the husband of Queen Victoria, Owen established the Natural History

Museum in South Kensington, London, to display the national collection of dinosaur fossils and other biological and geological exhibits.

In 1858, the first known American dinosaur was discovered, in marl pits in the small town of Haddonfield, New Jersey (although fossils had been found before, their nature had not been correctly discerned). The creature was named *Hadrosaurus foulkii*. It was an extremely important find: *Hadrosaurus* was one of the first nearly complete dinosaur skeletons found (the first was in 1834, in Maidstone, Kent, England), and it was clearly a bipedal creature. This was a revolutionary discovery as, until that point, most scientists had believed dinosaurs walked on four feet, like other lizards. Foulke's discoveries sparked a wave of dinosaur mania in the United States.



Othniel Charles Marsh, 19th century photograph



Edward Drinker Cope, 19th century photograph

Dinosaur mania was exemplified by the fierce rivalry between Edward Drinker Cope and Othniel Charles Marsh, both of whom raced to be the first to find new dinosaurs in what came to be known as the Bone Wars. The feud probably originated when Marsh publicly pointed out that Cope's reconstruction of an *Elasmosaurus* skeleton was flawed: Cope had inadvertently placed the plesiosaur's head at what should have been the animal's tail end. The fight between the two scientists lasted for over 30 years, ending in 1897 when Cope died after spending his entire fortune on the dinosaur hunt. Marsh 'won' the contest primarily because he was better funded through a relationship with the US Geological Survey. Unfortunately, many valuable dinosaur specimens were damaged or destroyed due to the pair's rough methods: for example, their diggers often used dynamite to unearth bones (a method modern paleontologists would find appalling). Despite their unrefined methods, the contributions of Cope and Marsh to paleontology were vast: Marsh unearthed 86 new species of dinosaur and Cope discovered 56, a total of 142 new species. Cope's collection is now at the American Museum of Natural History in New York, while Marsh's is on display at the Peabody Museum of Natural History at Yale University.

After 1897, the search for dinosaur fossils extended to every continent, including Antarctica. The first Antarctic dinosaur to be discovered, the ankylosaurid *Antarctopelta oliveroi*, was found on Ross Island in 1986, although it was 1994 before an Antarctic species, the theropod *Cryolophosaurus ellioti*, was formally named and described in a scientific journal.

Current dinosaur "hot spots" include southern South America (especially Argentina) and China. China in particular has produced many exceptional feathered dinosaur specimens due to the unique geology of its dinosaur beds, as well as an ancient arid climate particularly conducive to fossilization.

The "dinosaur renaissance"

The field of dinosaur research has enjoyed a surge in activity that began in the 1970s and is ongoing. This was triggered, in part, by John Ostrom's discovery of *Deinonychus*, an active predator that may have been warm-blooded, in marked contrast to the then-prevailing image of dinosaurs as sluggish and cold-blooded. Vertebrate paleontology has become a global science. Major new dinosaur discoveries have been made by paleontologists working in previously unexploited regions, including India, South America, Madagascar, Antarctica, and most significantly China (the amazingly well-preserved feathered dinosaurs in China have further consolidated the link between dinosaurs and their conjectured living descendants, modern birds). The widespread application of cladistics, which rigorously analyzes the relationships between biological organisms, has also proved tremendously useful in classifying dinosaurs. Cladistic analysis, among other modern techniques, helps to compensate for an often incomplete and fragmentary fossil record.

Cultural depictions

By human standards, dinosaurs were creatures of fantastic appearance and often enormous size. As such, they have captured the popular imagination and become an enduring part of human culture. Entry of the word "dinosaur" into the common vernacular reflects the animals' cultural importance: in English, "dinosaur" is commonly used to describe anything that is impractically large, slow-moving, obsolete, or bound for extinction.

Public enthusiasm for dinosaurs first developed in Victorian England, where in 1854, three decades after the first scientific descriptions of dinosaur remains, the famous dinosaur sculptures were unveiled in London's Crystal Palace Park. The Crystal Palace dinosaurs proved so popular that a strong market in smaller replicas soon developed. In subsequent decades, dinosaur exhibits opened at parks and museums around the world, ensuring that successive generations would be introduced to the animals in an immersive and exciting way. Dinosaurs' enduring popularity, in its turn, has resulted in significant public funding for dinosaur science, and has frequently spurred new discoveries. In the United States, for example, the competition between museums for public attention led directly to the Bone Wars of the 1880s and 1890s, during which a pair of feuding paleontologists made enormous scientific contributions.

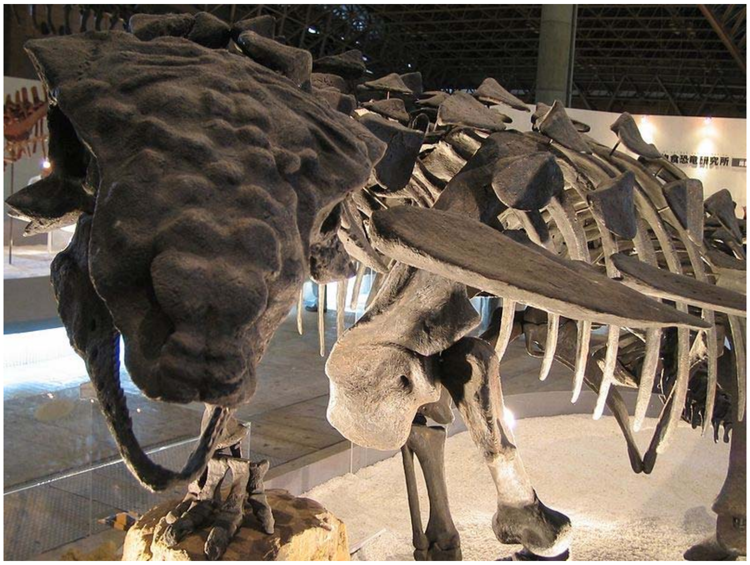
The popular preoccupation with dinosaurs has ensured their appearance in literature, film and other media. Beginning in 1852 with a passing mention in Charles Dickens' *Bleak House*, dinosaurs have been featured in large numbers of fictional works. Sir Arthur Conan Doyle's 1912 book *The Lost World*, the iconic 1933 film *King Kong*, 1954's *Godzilla* and its many sequels, the best-selling 1990 novel *Jurassic Park* by Michael Crichton and its 1993 film adaptation are just a few notable examples of dinosaur appearances in fiction. Authors of general-interest non-fictional works about dinosaurs, including some prominent paleontologists, have often sought to use the animals as a way to educate readers about science in general. Dinosaurs are ubiquitous in advertising; numerous companies have referenced dinosaurs in printed or televised advertisements, either in order to sell their own products or in order to characterize their rivals as slow-moving, dim-witted or obsolete.

Chapter- 2

Thyreophora and Ornithischia

Thyreophora

Thyreophorans
Fossil range: Early Jurassic-Late Cretaceous, 190–65.5 Ma



Mymoorapelta.

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Reptilia
Superorder:	Dinosauria
Order:	†Ornithischia
Suborder:	**†Thyreophora** Nopcsa, 1915

Infraorders

- †Ankylosauria
- †Stegosauria

The **Thyreophora** ("shield bearers", often known simply as "armored dinosaurs" - Greek: *θυρεος*, a large oblong shield, like a door and *φορεω*, I carry) were a subgroup of the ornithischian dinosaurs. They were armored herbivorous dinosaurs, living from the early Jurassic until the end of the Cretaceous.

Thyreophorans are characterized by the presence of body armor lined up in longitudinal rows along the body. Primitive forms had simple, low, keeled scutes or osteoderms whereas more derived forms developed more elaborate structures including spikes and plates. Most thyreophorans had relatively small brains for their body size.

Thyreophorans include well-known suborders such as the **Ankylosauria** and **Stegosauria** as well as lesser-known groups. Among the Ankylosauria, the two main groups are the Ankylosaurids and Nodosaurids. In both groups, the forelimbs were much shorter than the hindlimbs, and this was particularly exaggerated in stegosaurs. The clade has been defined as the group consisting of all species more closely related to *Ankylosaurus* than to *Triceratops*. Thyreophora is the sister group of the Cerapoda within the Genasauria.

Ankylosaurids are noted by the presence of a large tail club composed of distended vertebrae that have fused into a single mass. They were heavy-set and heavily armored from head to tail in bony armor, even down to minor features such as the eyelids. Spikes and nodules, often of horn, were set into the armor. The head was flat, stocky, with little or no "neck", roughly shovel-shaped and characterized by two spikes on either side of the head approximately where the ears and cheeks were. *Euoplocephalus tutus* is perhaps the best-known ankylosaurid.

Nodosaurids, the other family in the Ankylosauria, may actually include the ancestors of the ankylosaurids. They lived during the middle Jurassic (approx 170 mya) on up through the late Cretaceous (65 mya) and, while armored as the ankylosaurids, did not have a tail club. Instead, the bony bumps and spikes that covered the rest of their body continued out to the tail and/or were augmented with sharp spines. Two examples of nodosaurs are *Sauropelta* and *Edmontonia*, the latter most notable for its formidable forward-pointing shoulder spikes.

The **Stegosauria** suborder comprises the **Stegosauridae** and **Huayangosauridae**. These dinosaurs lived mostly from the Middle to Late Jurassic, although some fossils have been found in the Early Cretaceous. Stegosaurs had very small heads with simple, leaf-like teeth. Stegosaurs possessed rows of plates and/or spikes running down the dorsal midline and elongated dorsal vertebra. It has been suggested that stegosaur plates functioned in control of body temperature (thermoregulation) and/or were used as a display to identify members of a species, as well as to attract mates and intimidate rivals. Well known stegosaurs are *Stegosaurus* and *Kentrosaurus*.

Taxonomy

- **SUBORDER THYREOPHORA**
    - *Emausaurus*
    - *Scutellosaurus*
    - ?*Tatisaurus*
        - **Eurypoda**
            - **Infraorder Ankylosauria**
                - ?Family Scelidosauridae (may be basal group)
                    - *Bienosaurus*
                    - *Lusitanosaurus*
                    - *Scelidosaurus*
                - *Antarctopelta*
                - *Minmi*
                - Family Ankylosauridae
                - Family Nodosauridae
            - **Infraorder Stegosauria**
                - Family Huayangosauridae
                - Family Stegosauridae

"Tyreophorus"

"Tyreophorus" is an informal generic name, attributed to Friedrich von Huene, 1929, that is sometimes seen in lists of dinosaurs. It is probably a typographical error; von Huene intended to assign indeterminate remains to Thyreophora *incertae sedis*, but at some point in the process of publication, the text was revised to make it appear that he was creating a new generic name "Tyreophorus" (as described by George Olshevsky in a 1999 post to the Dinosaur Mailing List). The name is undescribed and has not been used seriously.

Ornithischia

Ornithischians
Fossil range:
Late Triassic–Late Cretaceous, 228–65 Ma

Edmontosaurus pelvis (showing ornithischian structure – left side) Oxford University Museum of Natural History

Scientific classification

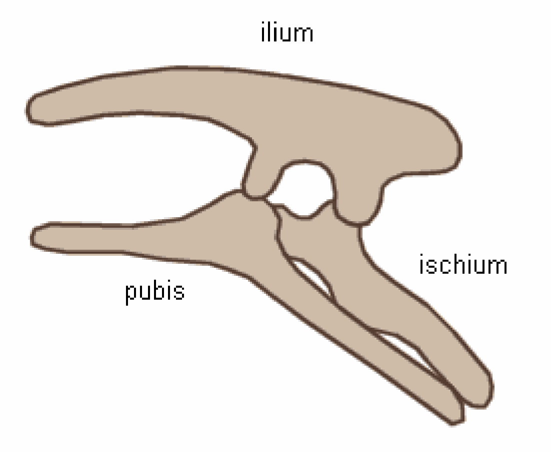
Kingdom:	Animalia
Phylum:	Chordata
Class:	Reptilia
Superorder:	Dinosauria
Order:	**†Ornithischia** Seeley, 1888

Subgroups

- †Fabrosauridae
- †Heterodontosauridae
- †Lesothosauridae
- †Pisanosauridae
- †Genasauria
    - †Cerapoda
    - †Thyreophora

Ornithischia or **Predentata** is an extinct order of beaked, herbivorous dinosaurs. The name *ornithischia* is derived from the Greek *ornitheos* (*ορνιθειος*) meaning 'of a bird' and *ischion* (*ισχιον*) meaning 'hip joint'. They are known as the 'bird-hipped' dinosaurs because of their bird-like hip structure, even though birds actually descended from the 'lizard-hipped' dinosaurs (the saurischians). Being herbivores that sometimes lived in herds, they were more numerous than the saurischians. They were prey animals for the theropods and were smaller than the sauropods.

Characteristics



Ornithischian pelvic structure (left side)

The Dinosauria superorder was divided into the two orders Ornithischia and Saurischia by Harry Seeley in 1887. This division, which has generally been accepted, is based on the evolution of the pelvis into a more bird-like structure (although birds did not descend from these dinosaurs), details in the vertebrae and armor and the possession of a 'predentary' bone. The predentary is an extra bone in the front of the lower jaw, which extends the dentary (the main lower jaw bone). The predentary coincides with the premaxilla in the upper jaw. Together they form a beak-like apparatus used to clip off plant material.

The ornithischian pubis bone points downward and toward the tail (backwards), parallel with the ischium, with a forward-pointing process to support the abdomen. This makes a four-pronged pelvic structure. In contrast to this, the saurischian pubis points downward and toward the head (forwards), as in ancestral lizard types. Ornithischians also had smaller antorbital fenestrae (holes in front of their eye sockets) than did saurischians, and a wider, more stable pelvis. A bird-like pubis arrangement, parallel to the vertebral column, evolved independently three times in dinosaur evolution, namely in the ornithischians, in the therizinosauroids and in bird-like dromaeosaurids.

Ornithischians shifted from bipedal to quadrupedal posture at least three times in their evolutionary history and have been shown to have been capable of adopting both postures early in their evolutionary history.

Classification

Taxonomy

Linnaean ranks after Benton (2004):

- **Order Ornithischia**
    - Genus *Eocursor*
    - Genus *Pisanosaurus*
    - Family Fabrosauridae
    - Family Heterodontosauridae
    - Family Lesothosauridae
    - **Suborder Thyreophora** – (armored dinosaurs)
        - Family Scelidosauridae
        - **Infraorder Stegosauria**
        - **Infraorder Ankylosauria**
    - **Suborder Cerapoda**
        - **Infraorder Ornithopoda**
            - Family Hypsilophodontidae*
            - Family Hadrosauridae – (duck-billed dinosaurs)
        - **Infraorder Pachycephalosauria**
        - **Infraorder Ceratopsia** – (horned dinosaurs)

Phylogeny

Genasaurian ornithischians are divided into two clades: the Thyreophora and the Cerapoda. The Thyreophora include the Stegosauria (like the armored *Stegosaurus*) and the Ankylosauria (like *Ankylosaurus*). The Cerapoda include the Marginocephalia (Ceratopsia like the frilled ceratopsidae and Pachycephalosauria) and the Ornithopoda (including duck-bills (hadrosaurs) such as *Edmontosaurus)*. The Cerapoda are a relatively recent concept (Sereno, 1986).

Chapter- 3

Saurischia (Type of Dinosaur)

Saurischians

Fossil range: Late Triassic-Recent 231.4–0 Ma

Tyrannosaurus rex saurischian pelvis and hind limbs (left side).

Scientific classification

Kingdom:	Animalia

Phylum:	Chordata
Class:	Reptilia
Superorder:	Dinosauria
Order:	**Saurischia** Seeley, 1888

Subgroups

- †Herrerasauridae?
- **Eusaurischia**
    - †Sauropodomorpha
    - Theropoda

Saurischia from the Greek *sauros* (*σαυρος*) meaning 'lizard' and *ischion* (*ισχιον*) meaning 'hip joint') is one of the two orders, or basic divisions, of dinosaurs. In 1888, Harry Seeley classified dinosaurs into two orders, based on their hip structure. Saurischians ('lizard-hipped') are distinguished from the ornithischians ('bird-hipped') by retaining the ancestral configuration of bones in the hip.

All carnivorous dinosaurs (the theropods) are saurischians, as are one of the two primary lineages of herbivorous dinosaurs, the sauropodomorphs. At the end of the Cretaceous Period, all non-avian saurischians became extinct. This is referred to as the Cretaceous-Tertiary extinction event. Avians (modern birds), as direct descendants of one group of theropod dinosaurs, are considered to be a sub-clade of saurischian dinosaurs in phylogenetic classification.

Description

Saurischians are distinguished from ornithischians by their three-pronged pelvic structure, with the pubis pointed forward. The ornithischians' pelvis is arranged with the pubis rotated backward, parallel with the ischium, often also with a forward-pointing process, giving a four-pronged structure.

The ornithischian hip structure is superficially similar to that of birds, which led Seeley to name them "**bird-hipped dinosaurs**," though he did not propose any specific relationship with birds. He termed saurischians "lizard-hipped" dinosaurs because they retained the ancestral hip anatomy also found in modern lizards.

However, as later study revealed, the hip structure possessed by modern birds actually evolved independently from the "lizard-hipped" saurischians (specifically, a sub-group of saurischians called the Maniraptora) in the Jurassic Period. In this example of convergent evolution, birds developed hips oriented similar to the earlier ornithischian hip anatomy, in both cases possibly as an adaptation to a herbivorous or omnivorous diet.

Classification

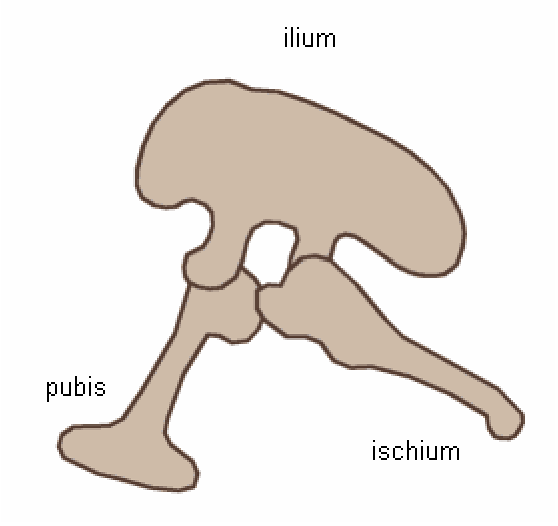


Diagram of saurischian pelvic structure (left side).

In his paper naming the two groups, Seeley reviewed previous classification schemes put forth by other paleontologists to divide up the traditional Order Dinosauria. He preferred one that had been put forward by Othniel Charles Marsh in 1878, which divided dinosaurs into four Orders: Sauropoda, Theropoda, Ornithopoda, and Stegosauria (these names are still used today in much the same way to refer to suborders or clades within Saurischia and Ornithischia).

Seeley, however, wanted to formulate a classification that would take into account a single primary difference between major dinosaurian groups based on a characteristic that also differentiated them from other reptiles. He found this in the configuration of the hip bones, and found that all four of Marsh's orders could be divided neatly into two major groups based on this feature. He placed the Stegosauria and Ornithopoda in the Ornithischia, and the Theropoda and Sauropoda in the Saurischia. Furthermore, Seeley used this major difference in the hip bones, along with many other noted differences between the two groups, to argue that "dinosaurs" were not a natural grouping at all, but rather two distinct orders that had arisen independently from more primitive archosaurs. This concept that "dinosaur" was an outdated term for two distinct orders lasted many decades in the scientific and popular literature, and it was not until the 1960s that scientists began to again consider the possibility that saurischians and ornithischians were more closely related to each other than they were to other archosaurs.

Although his concept of a paraphyletic Dinosauria is no longer accepted by most paleontologists, Seeley's basic division of the two dinosaurian groups has stood the test of time, and has been supported by modern cladistic analysis of relationships among dinosaurs. One alternate hypothesis challenging Seeley's classification was proposed by Robert T. Bakker in his 1986 book *The Dinosaur Heresies*. Bakker's classification separated the theropods into their own group and placed the two groups of herbivorous dinosaurs (the sauropodomorphs and ornithischians) together in a separate group he named the Phytodinosauria ('plant dinosaurs'). The Phytodinosauria hypothesis was based partly on the supposed link between ornithischians and prosauropods, and the idea that the former had evolved directly from the later, possibly by way of an enigmatic family that seemed to possess characters of both groups, the segnosaurs. However, it was later found that segnosaurs were actually an unusual type of herbivorous theropod saurischians closely related to birds, and the Phytodinosauria hypothesis fell out of favor.

Taxonomy

Mounted skeletons of *Tyrannosaurus* (left) and *Apatosaurus* (right) in the hall of saurischian dinosaurs at the American Museum of Natural History.

- **Order Saurischia**
    - Infraorder †Herrerasauria
        - **Suborder †Sauropodomorpha**
            - †Guaibasauridae
            - Infraorder †Prosauropoda
            - Infraorder †Sauropoda
        - **Suborder Theropoda**
            - *†Eoraptor*
            - *†Tawa*
            - Infraorder †Carnosauria
            - Infraorder †Ceratosauria
            - Infraorder †Deinonychosauria
            - Infraorder †Ornithomimosauria
            - Infraorder †Oviraptorosauria

Additionally, the genera *Teyuwasu* and *Agnosphitys* may represent early saurischians, or more primitive non-dinosaurs.

Chapter- 4

Theropoda (Type of Dinosaur)

Theropods
Fossil range:
Late Triassic–Late Cretaceous, 228–65 Ma
Descendant taxon Aves survives to present

Mounted replica of a *Tyrannosaurus rex* skeleton

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Reptilia
Superorder:	Dinosauria
Order:	Saurischia
(unranked):	Eusaurischia
Suborder:	**Theropoda** Marsh, 1881

Subgroups

- †*Eodromaeus*
- †*Eoraptor*?
- †Herrerasauridae?
- †*Tawa*
- **Avepoda**
  - †Coelophysoidea
  - **Neotheropoda**
    - †Ceratosauria
    - †Dilophosauridae
    - Tetanurae

Theropods suborder name *theropoda* meaning "beast feet") is both a suborder of bipedal saurischian dinosaurs, and a clade consisting of that suborder and its descendants (including modern birds). Dinosaurs belonging to the suborder *theropoda* were primarily carnivorous, although a number of theropod groups evolved herbivory, omnivory, and insectivory. Theropods first appeared during the Carnian age of the late Triassic period about 230 million years ago (Ma) and included the sole large terrestrial carnivores from the Early Jurassic until at least the close of the Cretaceous, about 65 Ma. In the Jurassic, birds evolved from small specialized coelurosaurian theropods, and are today represented by 9,900 living species.

Among the features linking theropod dinosaurs to birds are the three-toed foot, a furcula (wishbone), air-filled bones and (in some cases) feathers and brooding of the eggs.

Paleobiology

Diet

Specimen of the troodontid *Jinfengopteryx elegans*, with seeds preserved in the stomach region

While historically generalized as exclusively carnivorous dinosaurs, theropods in fact displayed a wide range of diets. All early finds of theropod fossils showed them to be primarily carnivorous. Theropod specimens known to scientists in the 19th and early 20th centuries all showed sharp teeth with serrated edges for cutting flesh, and some specimens even showed direct evidence of predatory behavior. For example, a *Compsognathus* fossil was found with a lizard in its stomach, and a *Velociraptor* specimen was found locked in combat with a *Protoceratops* (a type of ornithischian dinosaur).

The first confirmed non-carnivorous theropods found were the therizinosaurs, originally known as segnosaurs. First thought to be prosauropods, these enigmatic dinosaurs were later proven to be highly specialized, herbivorous theropods. Therizinosaurs possessed large abdomens for processing plant food, and small heads with beaks and leaf-shaped teeth. Further study of maniraptoran theropods and their relationships showed that therizinosaurs were not the only member of this group to abandon carnivory. Several other lineages of maniraptors show adaptations for an omnivorous diet, including seed-eating (some troodontids) and insect-eating (many avialans and alvarezsaurs). Oviraptorosaurs, ornithomimosaurs and advanced troodontids were likely omnivorous as well, and some theropods (such as *Masiakasaurus* and the spinosaurids) appear to have specialized in catching fish.

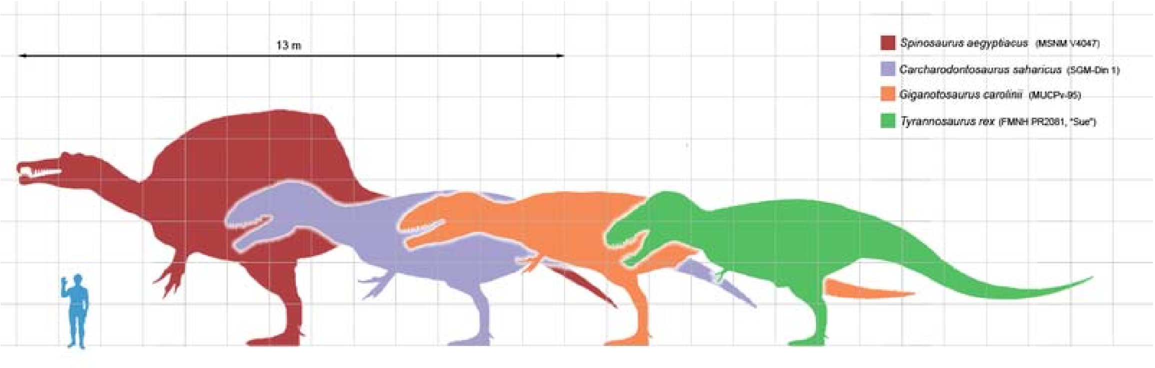
Skin, scales and feathers

Mesozoic theropods were also very diverse in terms of skin texture and covering. Though feather-like structures are known in the related ornithischian dinosaurs, evidence of feathers or feather-like structures has not been reported for any theropods less advanced than the coelurosaurs. More primitive theropods show evidence that their skin was covered in small, bumpy scales. In some species, these were interspersed with larger scales with bony cores, or osteoderms. This type of skin is best known in the ceratosaur *Carnotaurus*, which has been preserved with extensive skin impressions.

The most primitive known protofeathered theropods are the compsognathids and early tyrannosauroids, both coelurosaurs. These early forms had feathers which were relatively short and composed of simple, possibly branching filaments. Simple filaments are also seen in therizinosaurs, which also possessed large, stiffened "quill"-like feathers.

Most feathered theropods, including modern birds, usually retain scales only on the feet. Some forms seem to have mixed feathers elsewhere on the body as well. *Scansoriopteryx* preserved scales on the underside of the tail, and *Juravenator* may have been predominantly scaly with some simple filaments interspersed. On the other hand, some theropods were completely covered with feathers, such as the troodontid *Anchiornis*, which even had feathers on the feet and toes.

Size



Size comparison of selected giant theropod dinosaurs.

Tyrannosaurus was the largest and most popular theropod known to the general public for many decades. Since its discovery, however, a number of other giant carnivorous dinosaurs have been described, including *Spinosaurus*, *Carcharodontosaurus*, and *Giganotosaurus*. The original *Spinosaurus* specimens (as well as newer fossils described in 2006) support the idea that *Spinosaurus* is larger than *Tyrannosaurus*, showing that *Spinosaurus* was possibly 6 meters longer and at least 1 metric ton heavier than *Tyrannosaurus*. There is still no clear explanation for exactly why these animals grew so much larger than the predators that came before and after them.

The smallest non-avialan theropod known from adult specimens is the troodontid *Anchiornis huxleyi*, at 110 grams in weight and 34 centimeters (1 ft) in length. When modern birds are included, the Bee Hummingbird *Mellisuga helenae* is smallest at 1.9 g and 5.5 cm (2.2 in) long.

Nervous system and senses

Although rare, complete casts of theropod endocrania are known from fossils. Theropod endocrania can also be reconstructed from preserved brain cases without damaging valuable specimens by using a computed tomography scan and 3D reconstruction software. These finds are of evolutionary significance because they help document the emergence of the neurology of modern birds from that of earlier reptiles. An increase in the proportion of the brain occupied by the cerebrum seems to have occurred with the advent of the Coelurosauria and "continued throughout the evolution of maniraptorans and early birds."

Forelimb morphology

The clawed left hand of an *Allosaurus*.

Shortened forelimbs in relation to hind legs was a common trait among theropods, most notably in the abelisaurids (such as *Carnotaurus*) and the tyrannosaurids (such as *Tyrannosaurus*). This trait was, however, not universal: spinosaurids had well developed forelimbs, so also did many coelurosaurs. One genus, *Xuanhanosaurus*, has also been claimed to have been quadrupedal because of its comparatively robust forelimbs, but this is no longer thought to be likely.

The hands are also very different among the different groups. the most common is an appendage consisting of 3 fingers, the digits I, II and III (or possibly II, III and IV) with sharp claws. Some basal theropods (*Herrerasaurus*, *Eoraptor*) had 4 digits, and also a reduced metacarpal V. Ceratosaurians usually had 4 digits, while most tetanurans had 3.

The forelimbs' scope of use is also believed to have also been different among different families. The spinosaurids could have used their powerful forelimbs to hold fishes. Some small coelurosaurus (dromaeosaurids, scansoriopterygids) are believed to have used their forelimbs to climb in trees, and birds, which are believed to be descendants of theropods, use them for flight.

Forelimb movement

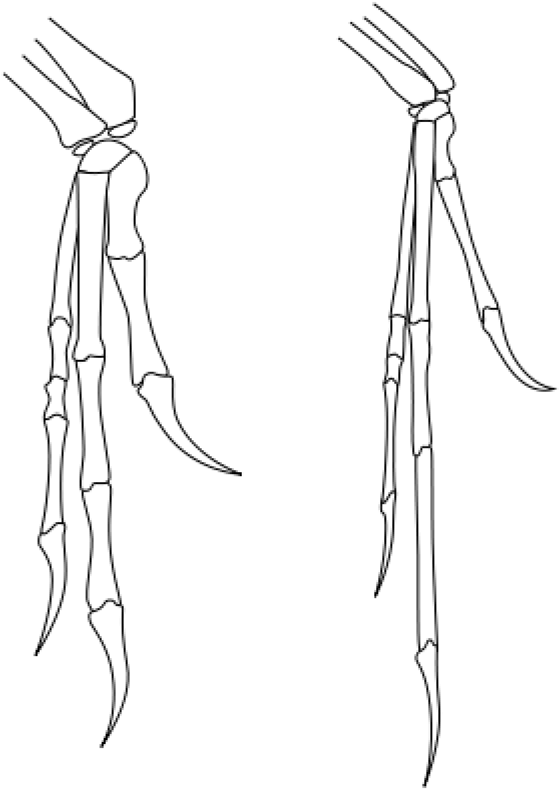
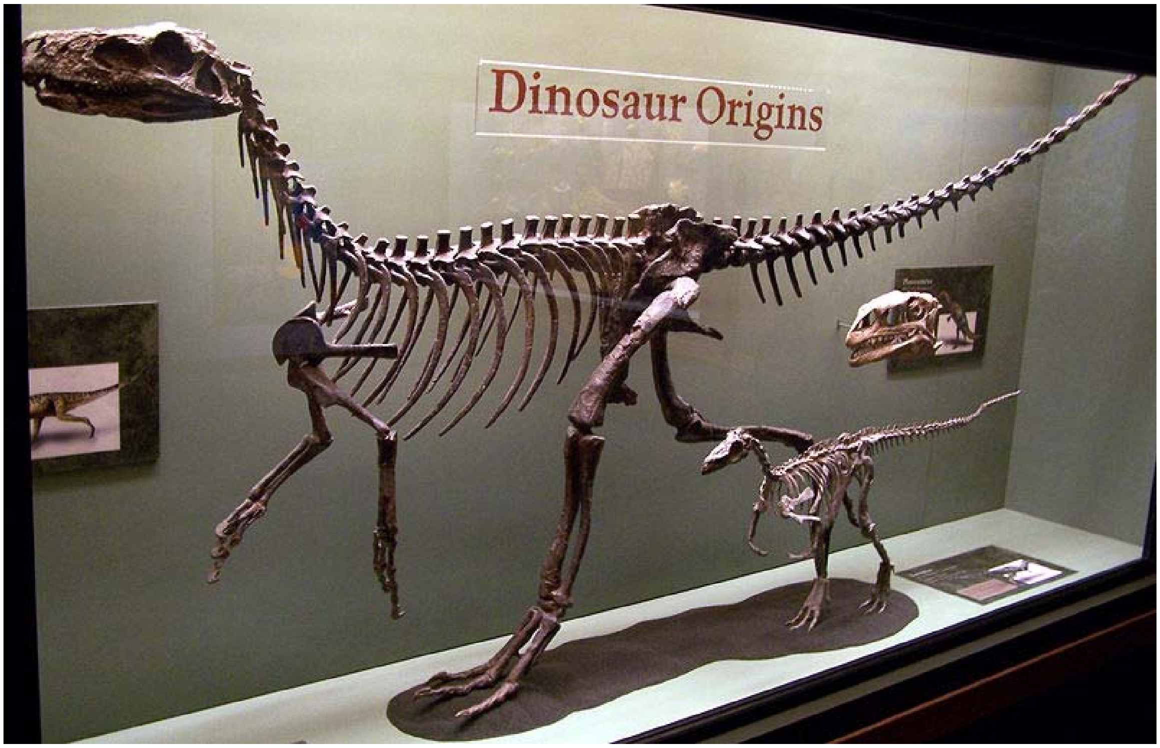


Diagram of *Deinonychus* (left) and *Archaeopteryx* (right) forelimbs illustrating wing-like posture

Contrary to the way theropods have often been reconstructed in art and the popular media, the range of motion of theropod forelimbs was severely limited, especially compared with the forelimb dexterity of humans and other primates. Most notably, theropods and other bipedal saurischian dinosaurs (including the bipedal prosauropods) could not pronate their hands—that is, they could not rotate the forearm so that the palms faced the ground or backwards towards the legs. In humans, pronation is achieved by motion of the radius relative to the ulna (the two bones of the forearm). In saurischian dinosaurs, however, the end of the radius near the elbow was actually locked into a groove of the ulna, preventing any movement. Movement at the wrist was also limited in many species, forcing the entire forearm and hand to move as a single unit with little flexibility. In theropods and prosauropods, the only way for the palm to face the ground would have been by lateral splaying of the entire forelimb, as in a bird raising its wing.

In carnosaurs like *Acrocanthosaurus*, the hand itself retained a relatively high degree of flexibility, with mobile fingers. This was also true of more basal theropods such as herrerasaurs and dilophosaurs. Coelurosaurs showed a shift in the use of the forearm, with greater flexibility at the shoulder allowing the arm to be raised towards the horizontal plane, and to even greater degrees in flying birds. However, in coelurosaurs such as ornithomimosaurs and especially dromaeosaurs, the hand itself had lost most flexibility, with highly inflexible fingers. Dromaeosaurs and other maniraptorans also showed increased mobility at the wrist not seen in other theropods, thanks to the presence of a specialized half-moon shaped wrist bone (the semi-lunate carpal) that allowed the whole hand to fold backward towards the forearm in the manner of modern birds.

Evolutionary history



The possible early forms *Herrerasaurus* (large) and *Eoraptor* (small)

During the late Triassic, a number of primitive proto-theropod and theropod dinosaurs existed and evolved alongside each other.

The earliest and most primitive of the theropod dinosaurs were the carnivorous *Eodromaeus* and the herrerasaurids of Argentina (as well as, possibly, the omnivorous *Eoraptor*). The herrerasaurs existed during the early late Triassic (Late Carnian to Early Norian). They were found in North America and South America and possibly also India and Southern Africa. The herrerasaurs were characterised by a mosaic of primitive and advanced features. Some paleontologists have in the past considered the herrerasaurians to be members of Theropoda, while other theorized the group to be basal saurischians, and may even have evolved prior to the saurischian-ornithischian split. Cladistic analysis following the discovery of *Tawa*, another Triassic dinosaur, suggests the herrerasaurs likely were early theropods.

The earliest and most primitive unambiguous theropods (or alternatively, "Eutheropoda" - 'True Theropods') are the Coelophysoidea. The Coelophysoidea were a group of widely distributed, lightly built and potentially gregarious animals. They included small hunters like *Coelophysis* and (possibly) larger predators like *Dilophosaurus*. These successful animals continued from the Late Carnian (early Late Triassic) through to the Toarcian (late Early Jurassic). Although in the early cladistic classifications they were included under the Ceratosauria and considered a side-branch of more advanced theropods, they may have been ancestral to all other theropods (which would make them a paraphyletic group).

The somewhat more advanced ceratosaurs (including *Ceratosaurus* and *Carnotaurus*) appeared during the Early Jurassic and continued through to the Late Jurassic in Laurasia. They competed alongside their more anatomically advanced tetanuran relatives and—in the form of the abelisaur lineage—lasted to the end of the Cretaceous in Gondwana.

The Tetanurae are more specialised again than the ceratosaurs. They are subdivided into the basal Megalosauroidea (alternately Spinosauroidea) and the more derived Avetheropoda. Megalosauridae were primarily Middle Jurassic to Early Cretaceous predators, and their spinosaurid relatives' remains are mostly from Early and Middle Cretaceous rocks. Avetheropoda, as their name indicates, were more closely related to birds and are again divided into the Allosauroidea (the diverse carcharodontosaurs) and the Coelurosauria (a very large and diverse dinosaur group including the birds).

Thus, during the late Jurassic, there were no fewer than four distinct lineages of theropods—ceratosaurs, megalosaurs, allosaurs, and coelurosaurs—preying on the abundance of small and large herbivorous dinosaurs. All four groups survived into the Cretaceous, and three of those—the ceratosaurs, coelurosaurs, and allosaurs—survived to end of the period, where they were geographically separate, the ceratosaurs and allosaurs in Gondwana, and the coelurosaurs in Laurasia.

Of all the theropod groups, the coelurosaurs were by far the most diverse. Some coelurosaur groups that flourished during the Cretaceous were the tyrannosaurids (including *Tyrannosaurus*) the dromaeosaurids (including *Velociraptor* and *Deinonychus*, which are remarkably similar in form to the oldest known bird, *Archaeopteryx*), the bird-like troodontids and oviraptorosaurs, the ornithomimosaurs (or "ostrich dinosaurs"), the strange giant-clawed herbivorous therizinosaurs, and the avialans, which include modern birds and is the only dinosaur lineage to survive the Cretaceous-Paleogene extinction event. While the roots of these various groups are found in the Middle Jurassic, they only became abundant during the Early Cretaceous. A few paleontologists, such as Gregory S. Paul, have suggested that some or all of these advanced theropods were actually descended from flying dinosaurs or proto-birds like *Archaeopteryx* that lost the ability to fly and returned to a terrestrial habitat.

Classification

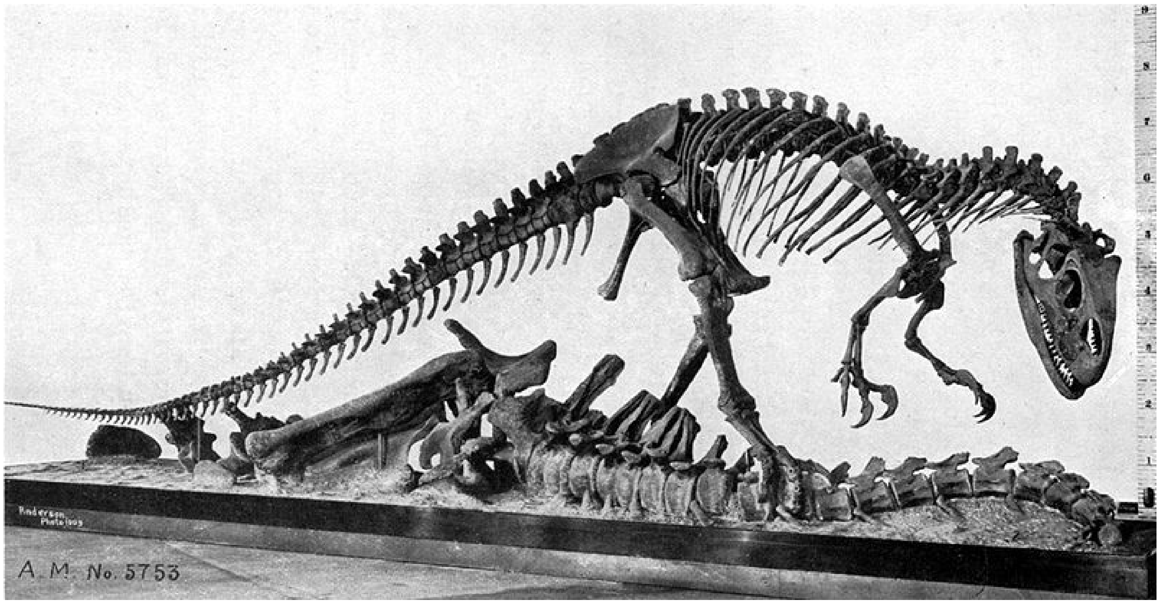
History of classification

Othniel Charles Marsh, who coined the name Theropoda. Photo c. 1870.

The name Theropoda (meaning "beast feet") was first coined by O.C. Marsh in 1881. Marsh initially named Theropoda as a suborder to include the family Allosauridae, but later expanded its scope, re-ranking it as an order to include a wide array of "carnivorous" dinosaur families, including Megalosauridae, Compsognathidae, Ornithomimidae, Plateosauridae and Anchisauridae (now known to be herbivorous prosauropods) and Hallopodidae (now known to be relatives of crocodilians). Due to the scope of Marsh's

Order Theropoda, it came to replace a previous taxonomic group that Marsh's rival E.D. Cope had created in 1866 for the carnivorous dinosaurs, **Goniopoda** ("angled feet").

By the early 20th century, some paleontologists, such as Friedrich von Huene, no longer considered carnivorous dinosaurs to have formed a natural group. Huene abandoned the name Theropoda, instead using Harry Seeley's Order Saurischia, which Huene divided into the suborders Coelurosauria and Pachypodosauria. Huene placed most of the small theropod groups into Coelurosauria, and the large theropods and prosauropods into Pachypodosauria, which he considered ancestral to the Sauropoda (prosauropods were still thought of as carnivorous at this time, owing to the incorrect association of rauisuchian skulls and teeth with prosauropod bodies, in animals such as *Teratosaurus*). In W.D. Matthew and Barnum Brown's 1922 description of the first known dromaeosaurid (*Dromaeosaurus albertensis*), they became the first paleontologists to exclude prosauropods from the carnivorous dinosaurs, and attempted to revive the name Goniopoda for that group, though neither of these suggestions were accepted by other scientists.



Allosaurus was one of the first dinosaurs classified as a theropod

It was not until 1956 that Theropoda came back into use as a taxon containing the carnivorous dinosaurs and their descendants, when Alfred Romer re-classified the Order Saurischia into two suborders, Theropoda and Sauropoda. This basic division has survived into modern paleontology, with the exception of, again, the Prosauropoda, which Romer included as an infraorder of theropods. Romer also maintained a division between Coelurosauria and Carnosauria (which he also ranked as infraorders). This dichotomy was upset by the discovery of *Deinonychus* and *Deinocheirus* in 1969, neither of which could be classified easily as "carnosaurs" or "coelurosaurs." In light of these and other discoveries, by the late 1970s Rinchen Barsbold created a new series of theropod infraorders: Coelurosauria, Deinonychosauria, Oviraptorosauria, Carnosauria, Ornithomimosauria, and Deinocheirosauria.

With the advent of cladistics and phylogenetic nomenclature in the 1980s, and their development in the 1990s and 2000s, a clearer picture of theropod relationships began to emerge. Several major theropod groups were named by Jacques Gauthier in 1986, including the clade Tetanurae for one branch of a basic theropod split with another group, the Ceratosauria. As more information about the link between dinosaurs and birds came to light, the more bird-like theropods were grouped in the clade Maniraptora (also named by Gauthier in 1986). These new developments also came with a recognition among most scientists that birds arose directly from maniraptoran theropods and, with the abandonment of ranks in cladistic classification, the re-evaluation of birds as a subset of theropod dinosaurs that happened to have survived the Mesozoic extinctions into the present.

Major groups

Ceratosaurus, a ceratosaur

Irritator, a spinosaur

Microraptor, a deinonychosaur

Theropods are a highly diverse group, and many major Mesozoic lineages have been identified:

- †Herrerasaurids, probably early theropods, though they may be more primitive saurischians or even non-dinosaurs
- †Coelophysoids, primitive theropods including *Coelophysis*
- †Ceratosaurians, including *Ceratosaurus* and abelisaurids. The latter were important Late Cretaceous predators in southern continents
- †Dilophosaurids, crested theropods sometimes allied with the coelophysoids
- Tetanurans, a major grouping of more advanced theropods
    - †Megalosauroids, including the crocodile-skulled spinosaurids
    - Avetheropods, more advanced and bird-like theropods
        - †Allosauroids, including *Allosaurus* and close relatives like the carcharodontosaurids
        - Coelurosaurians, a diverse lineage with a wide range of body sizes, diets and niches
            - †Tyrannosauroids, small to gigantic carnivores, often with reduced forelimbs
            - †Ornithomimosaurians, "ostrich-mimics", mostly toothless and probably omnivorous
            - Maniraptorans, birds and their closest relatives, all possessed feathers, many omnivorous or herbivorous
                - †Therizinosaurs, bipedal herbivores with large hand claws and small heads
                - †Alvarezsaurs, small bird-like insectivores with extremely short forelimbs
                - †Oviraptorosaurians, mostly toothless; their diet and lifestyle are uncertain
                - †Deinonychosaurs, popularly known as "raptors", extremely bird-like omnivores with some pure carnivores
                - Avialans, the group including modern birds (the only living dinosaurs) and other winged theropods
                    - †Scansoriopterygids, small insectivorous theropods that may have lived in trees
                    - Avians, traditional birds

Relationships

The following cladogram is adapted from Weishampel *et al.*, 2004. It retains Coelophysoidea as possible ceratosaurs, as opposed to many recent studies placing them outside ceratosaurs and ancestral to both ceratosaurs and tetanurae.

Chapter- 5

Feathered Dinosaur (Type of Dinosaur)

Artist's impression of *Anchiornis*, illustrating feather arrangement and colors

The realization that dinosaurs are closely related to birds raised the obvious possibility of **feathered dinosaurs**. Fossils of *Archaeopteryx* include well-preserved feathers, but it was not until the early 1990s that clearly non-avian dinosaur fossils were discovered with preserved feathers. Today more than twenty genera of dinosaurs, mostly theropods, are known to have been feathered. Most fossils are from the Yixian formation in China. The fossil feathers of one specimen, *Shuvuuia deserti*, have tested positive for beta-keratin, the main protein in bird feathers, in immunological tests.

Early hypotheses

The Berlin *Archaeopteryx*

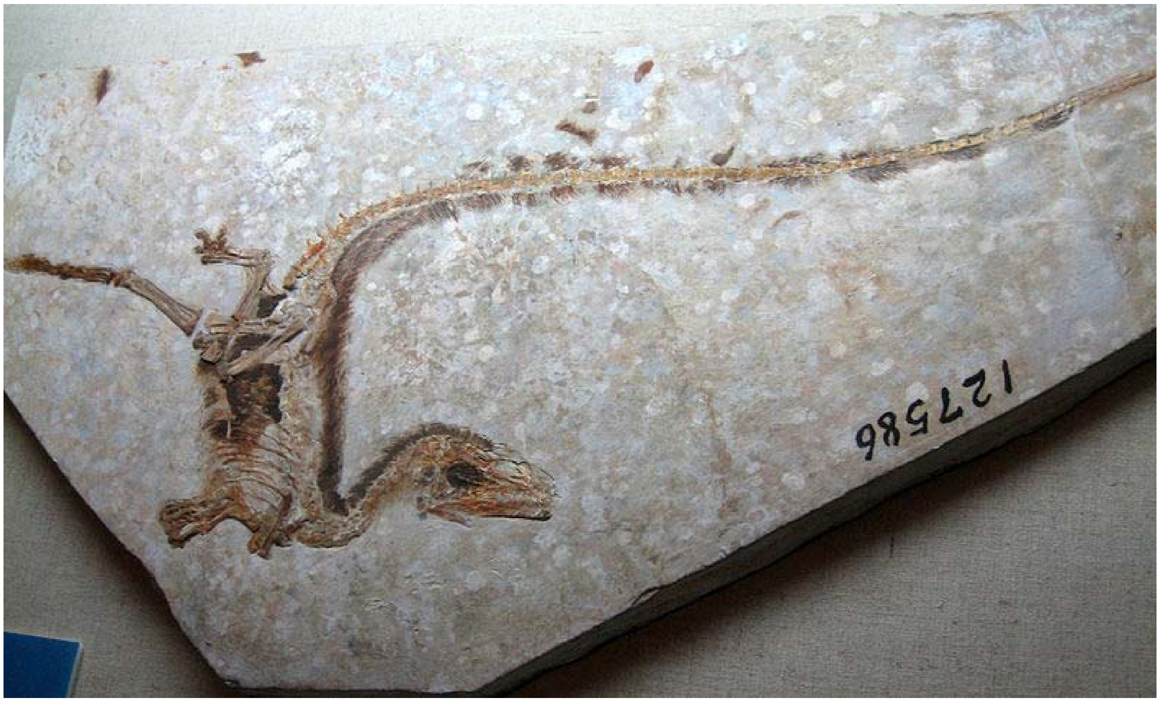
Shortly after the 1859 publication of Charles Darwin's *On the Origin of Species*, British biologist and evolution-defender Thomas Henry Huxley proposed that birds were descendants of dinosaurs. He compared the skeletal structure of *Compsognathus*, a small theropod dinosaur, and the 'first bird' *Archaeopteryx lithographica* (both of which were found in the Upper Jurassic Bavarian limestone of Solnhofen). He showed that, apart from its hands and feathers, *Archaeopteryx* was quite similar to *Compsognathus*. In 1868 he published *On the Animals which are most nearly intermediate between Birds and Reptiles*, making the case. The leading dinosaur expert of the time, Richard Owen, disagreed, claiming *Archaeopteryx* as the first bird outside dinosaur lineage. For the next century, claims that birds were dinosaur descendants faded, with more popular birdancestry hypotheses including 'crocodylomorph' and 'thecodont' ancestors, rather than dinosaurs or other archosaurs.

In 1964, John Ostrom described *Deinonychus antirrhopus*, a theropod whose skeletal resemblance to birds seemed unmistakable. Ostrom became a leading proponent of the theory that birds are direct descendants of dinosaurs. Further comparisons of bird and dinosaur skeletons, as well as cladistic analysis strengthened the case for the link, particularly for a branch of theropods called maniraptors. Skeletal similarities include the neck, the pubis, the wrists (semi-lunate carpal), the 'arms' and pectoral girdle, the shoulder blade, the clavicle and the breast bone. In all, over a hundred distinct anatomical features are shared by birds and theropod dinosaurs.

Other researchers drew on these shared features and other aspects of dinosaur biology and began to suggest that at least some theropod dinosaurs were feathered. The first restoration of a feathered dinosaur was Sarah Landry's depiction of a feathered "Syntarsus" (now renamed *Megapnosaurus* or considered a synonym of *Coelophysis*), in Robert T. Bakker's 1975 publication *Dinosaur Renaissance*. Gregory S. Paul was probably the first paleoartist to depict maniraptoran dinosaurs with feathers and protofeathers, starting in the late 1970s.

By the 1990s, most paleontologists considered birds to be surviving dinosaurs and referred to 'non-avian dinosaurs' (all extinct), to distinguish them from birds (aves). Before the discovery of feathered dinosaurs, the evidence was limited to Huxley and Ostrom's comparative anatomy. Some mainstream ornithologists, including Smithsonian Institution curator Storrs L. Olson, disputed the links, specifically citing the lack of fossil evidence for feathered dinosaurs.

Fossil evidence



Sinosauropteryx fossil, first fossil of a non-avian dinosaur with feathers

After a century of hypotheses without conclusive evidence, well-preserved fossils of feathered dinosaurs were discovered during the 1990s, and more continue to be found. The fossils were preserved in a Lagerstätte — a sedimentary deposit exhibiting remarkable richness and completeness in its fossils — in Liaoning, China. The area had repeatedly been smothered in volcanic ash produced by eruptions in Inner Mongolia 124 million years ago, during the Early Cretaceous Period. The fine-grained ash preserved the living organisms that it buried in fine detail. The area was teeming with life, with millions of leaves, angiosperms (the oldest known), insects, fish, frogs, salamanders, mammals, turtles, lizards and crocodilians discovered to date.

The most important discoveries at Liaoning have been a host of feathered dinosaur fossils, with a steady stream of new finds filling in the picture of the dinosaur-bird connection and adding more to theories of the evolutionary development of feathers and flight. Norell et al. (2007) reported quill knobs from an ulna of *Velociraptor mongoliensis*, and these are strongly correlated with large and well-developed secondary feathers.

A nesting *Citipati osmolskae* specimen, at the AMNH.

Behavioural evidence, in the form of an oviraptorosaur on its nest, showed another link with birds. Its forearms were folded, like those of a bird. Although no feathers were preserved, it is likely that these would have been present to insulate eggs and juveniles.

Genuine feathers?

There have been claims that the supposed feathers of the Chinese fossils were a preservation artifact. Despite doubts, the fossil feathers have roughly the same appearance as those of birds fossilized in the same locality, so there is no serious reason to think they are of different nature; moreover, no non-theropod fossil from the same site shows such an artifact, but sometimes show unambiguous hair (some mammals) or scales (some reptiles).

The "Archaeoraptor" fake

In 1999, a supposed 'missing link' fossil of an apparently feathered dinosaur named "Archaeoraptor liaoningensis", found in Liaoning Province, northeastern China, turned out to be a forgery. Comparing the photograph of the specimen with another find, Chinese paleontologist Xu Xing came to the conclusion that it was composed of two portions of different fossil animals. His claim made *National Geographic* review their research and they too came to the same conclusion. The bottom portion of the "Archaeoraptor" composite came from a legitimate feathered dromaeosaurid now known as *Microraptor*, and the upper portion from a previously-known primitive bird called *Yanornis*.

Current knowledge

List of dinosaur genera preserved with evidence of feathers

Fossil of *Sinornithosaurus millenii*, the first evidence of feathers in dromaeosaurids.

Fossil cast of NGMC 91, a probable specimen of *Sinornithosaurus*.

Jinfengopteryx elegans fossil

A number of non-avian dinosaurs are now known to have been feathered. Direct evidence of feathers exists for the following genera, listed in the order currently accepted evidence was first published. In all examples, the evidence described consists of feather impressions, except those marked with an asterisk (*), which denotes genera known to have had feathers based on skeletal or chemical evidence, such as the presence of quill knobs.

1. *Avimimus** (1987)
2. *Sinosauropteryx* (1996)
3. *Protarchaeopteryx* (1997)
4. *Caudipteryx* (1998)
5. *Rahonavis** (1998)
6. *Shuvuuia* (1999)
7. *Sinornithosaurus* (1999)
8. *Beipiaosaurus* (1999)
9. *Microraptor* (2000)
10. *Nomingia** (2000)

11. *Cryptovolans* (2002)
12. *Scansoriopteryx* (2002)
13. *Psittacosaurus*? (2002)
14. *Yixianosaurus* (2003)
15. *Dilong* (2004)
16. *Pedopenna* (2005)
17. *Jinfengopteryx* (2005)
18. *Juravenator* (2006)
19. *Sinocalliopteryx* (2007)
20. *Velociraptor** (2007)
21. *Similicaudipteryx* (2008)
22. *Epidexipteryx* (2008)
23. *Anchiornis* (2009)
24. *Tianyulong*? (2009)
25. *Concavenator**? (2010)

- The ornithmomimosaur *Pelecanimimus* was initially reported to preserve filamentous feathers. However, subsequent detailed study of the structure showed them to be muscle fibers.

- Note, filamentous structures in some ornithischian dinosaurs (*Psittacosaurus*, *Tianyulong*) and pterosaurs may or may not be homologous with the feathers and protofeathers of theropods.

Primitive feather types

The evolution of feather structures is thought to have proceeded from simple hollow filaments through several stages of increasing complexity, ending with the large, deeply rooted, feathers with strong pens (rachis), barbs and barbules that birds display today.

Some evidence suggests that the original function of simple feathers was insulation. In particular, preserved patches of skin in large, derived, tyrannosauroids show scutes, while those in smaller, more primitive, forms show feathers. This may indicate that the larger forms had complex skins, with both scutes and filaments, or that tyrannosauroids may be like rhinos and elephants, having filaments at birth and then losing them as they developed to maturity. An adult *Tyrannosaurus rex* weighed about as much as an African Elephant. If large tyrannosauroids were endothermic, they would have needed to radiate heat efficiently, and feathers would have interfered with this.

It is not known with certainty at what point in archosaur phylogeny the earliest simple “protofeathers” arose, or if they arose once or, independently, multiple times. Filamentous structures are clearly present in pterosaurs, and long, hollow quills have been reported in specimens of the ornithischian dinosaurs *Psittacosaurus* and *Tianyulong*. In 2009 Xu et al. noted that the hollow, unbranched, stiff integumentary structures found on a specimen of *Beipiaosaurus* were strikingly similar to the integumentary structures of *psittacosaurus* and pterosaurs. They suggested that all of these structures may have been inherited from a common ancestor much earlier in the evolution of archosaurs, possibly in an ornithodire from the Middle Triassic or earlier.

Display feathers are also known from dinosaurs that are very primitive members of the bird lineage, or Avialae. The most primitive example is *Epidexipteryx*, which had a short tail with extremely long, ribbon - like, feathers. Oddly enough, the fossil does not preserve wing feathers, suggesting that *Epidexipteryx* was either secondarily flightless, or that display feathers evolved before flight feathers in the bird lineage.

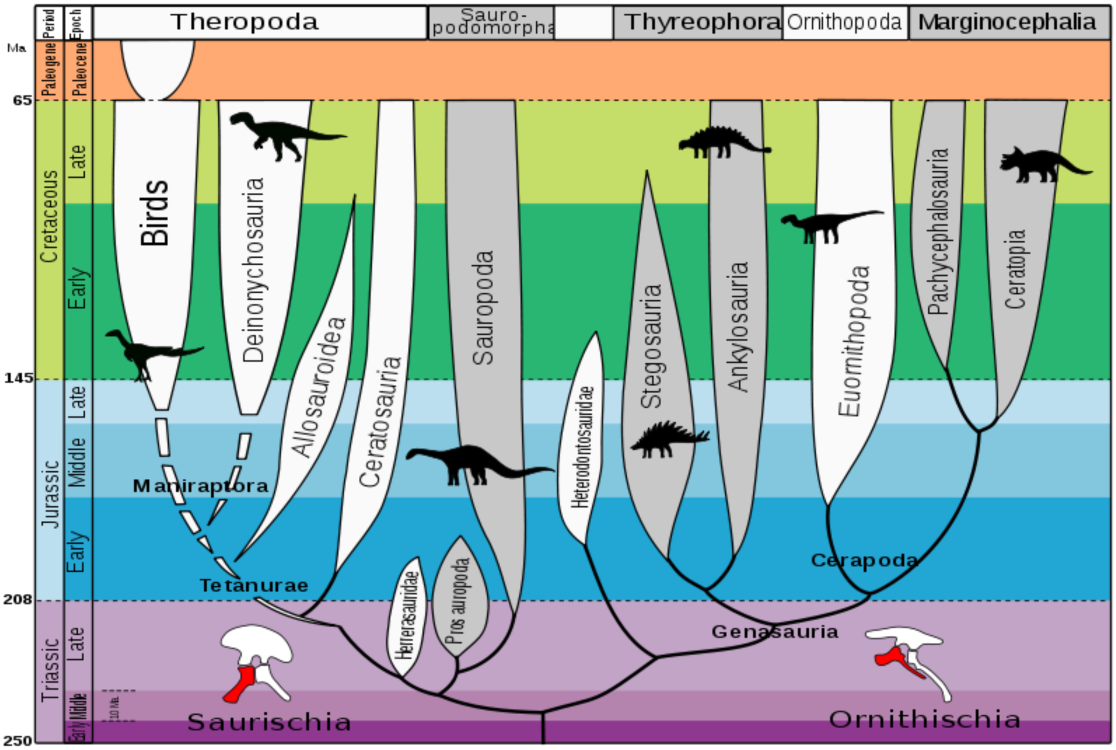
Phylogeny and the inference of feathers in other dinosaurs

Fossil feather impressions are extremely rare and they require exceptional preservation conditions to form. Therefore only a few feathered dinosaur genera have been identified so far. However, through a process called phylogenetic bracketing, scientists can infer the presence of feathers on poorly-preserved specimens. All fossil feather specimens have been found to show certain similarities. Due to these similarities and through developmental research almost all scientists agree that feathers could only have evolved once in dinosaurs. Feathers would then have been passed down to all later, more derived species (although it is possible that some lineages lost feathers secondarily). If a dinosaur falls at a point on an evolutionary tree within the known feather-bearing lineages, scientists assume it too had feathers, unless conflicting evidence is found. This technique can also be used to infer the type of feathers a species may have had, since the developmental history of feathers is now reasonably well-known.

The scientists who described the (apparently unfeathered) *Juravenator* performed a genealogical study of coelurosaurs, including distribution of various feather types. Based on the placement of feathered species in relation to those that have not been found with any type of skin impressions, they were able to infer the presence of feathers in certain dinosaur groups. The following simplified cladogram follows these results, and shows the likely distribution of plumaceous (downy) and pennaceous (vaned) feathers among theropods. Note that the authors inferred pennaceous feathers for *Velociraptor* based on phylogenetic bracketing, a prediction later confirmed by fossil evidence.

Chapter- 6

Dinosaur Classification



Classification of dinosaurs

Dinosaur classification began in 1842 when Sir Richard Owen placed *Iguanodon*, *Megalosaurus*, and *Hylaeosaurus* in "a distinct tribe or suborder of Saurian Reptiles, for which I would propose the name of Dinosauria." In 1887 and 1888 Harry Seeley divided dinosaurs into the two orders Saurischia and Ornithischia, based on their hip structure. These divisions have proved remarkably enduring, even through several seismic changes in the taxonomy of dinosaurs.

The largest change was prompted by entomologist Willi Hennig's work in the 1950s, which evolved into modern cladistics. For specimens known only from fossils, the rigorous analysis of characters to determine evolutionary relationships between different groups of animals (*clades*) proved incredibly useful. When computer-based analysis using cladistics came into its own in the 1990s, paleontologists became among the first zoologists to almost wholeheartedly adopt the system. Progressive scrutiny and work upon dinosaurian interrelationships, with the aid of new discoveries that have shed light on previously uncertain relationships between taxa, have begun to yield a stabilizing classification since the mid-2000s. While cladistics is the predominant classificatory system among paleontology professionals, the Linnean system is still in use, especially in works intended for popular distribution.

Benton classification

As most paleontologists have advocated a shift away from traditional, ranked Linnaean taxonomy in favor of rankless phylogentic systems, few ranked taxonomies of dinosaurs have been published since the 1980s. The following schema is among the most recent, from the third edition of *Vertebrate Palaeontology*, a respected undergraduate textbook. While it is structured so as to reflect evolutionary relationships (similar to a cladogram), it also retains the traditional ranks used in Linnaean taxonomy. The classification has been updated from the second edition in 2000 to reflect new research, but remains fundamentally conservative.

Benton classifies all dinosaurs within the Series Amniota, Class Sauropsida, Subclass Diapsida, Infraclass Archosauromorpha, Division Archosauria, Subdivision Avemetatarsalia, Infradivision Ornithodira, and Superorder Dinosauria. Dinosauria is then divided into the two traditional orders, Saurischia and Ornithischia. The cross (†) is used to indicate taxa with no living members.

Order Saurischia

- **Suborder Theropoda**
    - †Infraorder Herrerasauria
    - †Infraorder Coelophysoidea
    - †Infraorder Ceratosauria
        - †Family Ceratosauridae
        - †Family Abelisauridae
    - Infraorder Tetanurae
        - †Division Carnosauria
            - †Sudivision Spinosauroidea
                - †Family Megalosauridae
                - †Family Spinosauridae
            - †Subdivision Allosauroidea
                - †Family Allosauridae
                - †Family Carcharodontosauridae
        - Division Coelurosauria
            - †Family Coeluridae
            - Subdivision Maniraptoriformes

                - †Family Tyrannosauridae
                - †Family Ornithomimidae
                - Infradivision Maniraptora
                    - †Family Alvarezsauridae
                    - †Family Therizinosauridae
                    - †Cohort Deinonychosauria
                        - †Family Troodontidae
                        - †Family Dromaeosauridae
                        - Class Aves
- **†Suborder Sauropodomorpha**
    - †*Thecodontosaurus*
    - †Family Plateosauridae
    - †*Riojasaurus*
    - †Family Massospondylidae
    - †Infraorder Sauropoda
        - †Family Vulcanodontidae
        - †Family Omeisauridae
        - †Division Neosauropoda
            - †Family Cetiosauridae
            - †Family Diplodocidae
            - †Subdivision Macronaria
                - †Family Camarasauridae
                - †Infradivision Titanosauriformes
                    - †Family Brachiosauridae
                    - †Cohort Somphospondyli
                        - †Family Euhelopodidae
                        - †Family Titanosauridae

†Order Ornithischia

- †Family Pisanosauridae
- †Family Fabrosauridae
- **†Suborder Thyreophora**
    - †Family Scelidosauridae
    - †Infraorder Stegosauria
    - †Infraorder Ankylosauria
        - †Family Nodosauridae
        - †Family Ankylosauridae
- **†Suborder Cerapoda**
    - †Infraorder Pachycephalosauria
    - †Infraorder Ceratopsia
        - †Family Psittacosauridae
        - †Family Protoceratopsidae
        - †Family Ceratopsidae
    - †Infraorder Ornithopoda
        - †Family Heterodontosauridae

- †Family Hypsilophodontidae
- †Family Iguanodontidae *
- †Family Hadrosauridae

Weishampel/Dodson/Osmólska classification

The following is based on the second edition of *The Dinosauria*, a compilation of articles by experts in the field that provided the most comprehensive coverage of Dinosauria available when it was first published in 1990. The second edition updates and revises that work.

The cladogram and phylogenetic definitions below reflect the current understanding of evolutionary relationships. The taxa and symbols in parentheses after a given taxa define these relationships. The plus symbol ("+") between taxa indicates the given taxa is a node-based clade, defined as comprising all descendants of the last common ancestor of the "added" taxa. The greater-than symbol (">") indicates the given taxon is a stem-based taxon, comprising all organisms sharing a common ancestor that is not also an ancestor of the "lesser" taxon.

Saurischia

(*Tyrannosaurus*/*Allosaurus* > *Triceratops*/*Stegosaurus*)

- Herrerasauria (*Herrerasaurus* > *Liliensternus*, *Plateosaurus*)
    - Herrerasauridae (*Herrerasaurus* + *Staurikosaurus*)
- ? *Eoraptor lunensis*
- **Sauropodomorpha** (*Saltasaurus* > Theropoda)
    - ? *Saturnalia tupiniquim*
    - ? Thecodontosauridae
    - Prosauropoda (*Plateosaurus* > Sauropoda)
        - ? Thecodontosauridae
        - ? Anchisauria (*Anchisaurus* + *Melanorosaurus*)
            - ? Anchisauridae (*Anchisaurus* > Melanorosaurus)
            - ? Melanorosauridae (*Melanorosaurus* > *Anchisaurus*)
        - Plateosauria (*Jingshanosaurus* + *Plateosaurus*)
            - Massospondylidae
            - Yunnanosauridae
            - Plateosauridae (*Plateosaurus* > *Yunnanosaurus*, *Massospondylus*)
    - Sauropoda (*Saltasaurus* > *Plateosaurus*)
        - ? Anchisauridae
        - ? Melanorosauridae
        - Blikanasauridae
        - Vulcanodontidae
        - Eusauropoda (*Shunosaurus* + *Saltasaurus*)
            - ? Euhelopodidae

      - Mamenchisauridae
      - Cetiosauridae (*Cetiosaurus* > *Saltasaurus*)
      - Neosauropoda (*Diplodocus* + *Saltasaurus*)
        - Diplodocoidea (*Diplodocus* > *Saltasaurus*)
          - Rebbachisauridae (*Rebbachisaurus* > *Diplodocus*)
          - Flagellicaudata
            - Dicraeosauridae (*Dicraeosaurus* > *Diplodocus*)
            - Diplodocidae (*Diplodocus* > *Dicraeosaurus*)
        - Macronaria (*Saltasaurus* > *Diplodocus*)
          - ? *Jobaria tiguidensis*
          - Camarasauromorpha (*Camarasaurus* + *Saltasaurus*)
            - Camarasauridae
            - Titanosauriformes (*Brachiosaurus* + *Saltasaurus*)
              - Brachiosauridae (*Brachiosaurus* > *Saltasaurus*)
              - Titanosauria (*Saltasaurus* > *Brachiosaurus*)
                - Andesauridae
                - Lithostrotia (*Malawisaurus* + *Saltasaurus*)
                  - *Isisaurus colberti*
                  - *Paralititan stromeri*
                  - Nemegtosauridae
                  - Saltasauridae (*Opisthocoelicaudia* + *Saltasaurus*)

- **Theropoda** (*Passer domesticus* > *Cetiosaurus oxoniensis*)
  - ? *Eoraptor lunensis*
  - ? Herrerasauridae
  - Ceratosauria (*Ceratosaurus nasicornis* > Aves)
    - ? Coelophysoidea (*Coelophysis* > *Ceratosaurus*)
      - ? *Dilophosaurus wetherilli*
      - Coelophysidae (*Coelophysis* + *Megapnosaurus*)

  - ? Neoceratosauria (*Ceratosaurus* > *Coelophysis*)
    - Ceratosauridae
    - Abelisauroidea (*Carnotaurus sastrei* > *C. nasicornis*)
      - Abelisauria (*Noasaurus* + *Carnotaurus*)
        - Noasauridae
        - Abelisauridae (*Abelisaurus comahuensis* + *C. sastrei*)
          - Carnotaurinae (*Carnotaurus* > *Abelisaurus*)
          - Abelisaurinae (*Abelisaurus* > *Carnotaurus*)
- Tetanurae (*P. domesticus* > *C. nasicornis*)
  - ? Spinosauroidea (*Spinosaurus aegyptiacus* > *P. domesticus*)
    - Megalosauridae (*Megalosaurus bucklandii* > *P. domesticus*, *S. aegyptiacus*, *Allosaurus fragilis*)
      - Megalosaurinae (*M. bucklandii* > *Eustreptospondylus oxoniensis*)
      - Eustreptospondylinae (*E. oxoniensis* > *M. bucklandii*)
    - Spinosauridae (*S. aegyptiacus* > *P. domesticus*, *M. bucklandii*, *A. fragilis*)
      - Baryonychinae (*Baryonyx walkeri* > *S. aegyptiacus*)
      - Spinosaurinae (*S. aegyptiacus* > *B. walkeri*)
  - Avetheropoda (*A. fragilis* + *P. domesticus*)
    - Carnosauria (*A. fragilis* > Aves)
      - ? Spinosauroidea
      - *Monolophosaurus jiangi*
      - Allosauroidea (*A. fragilis* + *Sinraptor dongi*)
        - Allosauridae (*A. fragilis* > *S. dongi*, *Carcharodontosaurus saharicus*)
        - Sinraptoridae (*S. dongi* > *A. fragilis*, *C. saharicus*)
        - Carcharodontosauridae (*C. saharicus* > *A. fragilis*, *S. dongi*)
    - Coelurosauria (*P. domesticus* > *A. fragilis*)
      - Compsognathidae (*Compsognathus longipes* > *P. domesticus*)
      - *Proceratosaurus bradleyi*
      - *Ornitholestes hermanni*
      - Tyrannoraptora (*Tyrannosaurus rex* + *P. domesticus*)
        - *Coelurus fragilis*
        - Tyrannosauroidea (*T. rex* > *Ornithomimus velox*, *Deinonychus antirrhopus*, *A. fragilis*)
          - Dryptosauridae

  - Tyrannosauridae (*T. rex* + *Tarbosaurus bataar* + *Daspletosaurus torosus* + *Albertosaurus sarcophagus* + *Gorgosaurus libratus*)
    - Tyrannosaurinae (*T. rex* > *A. sarcophagus*)
    - Albertosaurinae (*A. sarcophagus* > *T. rex*)
- Maniraptoriformes (*O. velox* + *P. domesticus*)
  - Ornithomimosauria (*Ornithomimus edmontonicus* + *Pelecanimimus polyodon*)
    - Harpymimidae
    - Garudimimidae
    - Ornithomimidae
  - Maniraptora (*P. domesticus* > *O. velox*)
    - Oviraptorosauria (*Oviraptor philoceratops* > *P. domesticus*)
      - Caenagnathoidea (*O. philoceratops* + *Caenagnathus collinsi*)
        - Caenagnathidae (*C. collinsi* > *O. philoceratops*)
        - Oviraptoridae (*O. philoceratops* > *C. collinsi*)
          - Oviraptorinae (*O. philoceratops* + *Citipai osmolskae*)

                - Therizinosauroidea (*Therizinosaurus* + *Beipiaosaurus*)
                  - Alxasauridae
                  - Therizinosauridae
              - Paraves (*P. domesticus* > *O. philoceratops*)
                - Eumaniraptora (*P. domesticus* + *D. antirrhopus*)
                  - Deinonychosauria (*D. antirrhopus* > *P. domesticus* or *Dromaeosaurus albertensis* + *Troodon formosus*)
  - Troodontidae (*T. formosus* > *Velociraptor mongoliensis*)
  - Dromaeosauridae (*Microraptor zhaoianus* + *Sinornithosaurus millenii* + *V. mongoliensis*)
- Avialae (*Archaeopteryx* + Neornithes)

Ornithischia

(*Iguanodon*/*Triceratops* > *Cetiosaurus*/*Tyrannosaurus*)

- ? *Lesothosaurus diagnosticus*
- ? Heterodontosauridae
- Genasauria (*Ankylosaurus* + *Triceratops*)
  - **Thyreophora** (*Ankylosaurus* > *Triceratops*)
    - Scelidosauridae
    - Eurypoda (*Ankylosaurus* + *Stegosaurus*)
      - Stegosauria (*Stegosaurus* > *Ankylosaurus*)
        - Huayangosauridae (*Huayangosaurus* > *Stegosaurus*)
        - Stegosauridae (*Stegosaurus* > *Huayangosaurus*)
          - *Dacentrurus armatus*
          - Stegosaurinae (*Stegosaurus* > *Dacentrurus*)
      - Ankylosauria (*Ankylosaurus* > *Stegosaurus*)
        - Ankylosauridae (*Ankylosaurus* > *Panoplosaurus*)

        - *Gastonia burgei*
        - *Shamosaurus scutatus*
        - Ankylosaurinae (*Ankylosaurus* > *Shamosaurus*)
      - Nodosauridae (*Panoplosaurus* > *Ankylosaurus*)
- **Cerapoda** (*Triceratops* > *Ankylosaurus*)
  - Ornithopoda (*Edmontosaurus* > *Triceratops*)
    - ? *Lesothosaurus diagnosticus*
    - ? Heterodontosauridae
    - Euornithopoda
      - *Hypsilophodon foxii*
      - *Thescelosaurus neglectus*
      - Iguanodontia (*Edmontosaurus* > *Thescelosaurus*)
        - *Tenontosaurus tilletti*
        - Rhabdodontidae
        - Dryomorpha
          - Dryosauridae
          - Ankylopollexia
            - Camptosauridae
            - Styracosterna
              - *Lurdusaurus arenatus*
              - Iguanodontoidea (=Hadrosauriformes)

                - Iguanodontide
                - Hadrosauridae (*Telmatosaurs* + *Parasaurolophus*)
                  - *Telmatosaurs transsylvanics*
                  - Euhadrosauria
  - Lambeosaurinae
  - Saurolophinae (=Hadrosaurinae)

  - Marginocephalia
    - Pachycephalosauria (*Pachycephalosaurus wyomingensis* > *Triceratops horridus*)
      - Goyocephala (*Goyocephale* + *Pachycephalosaurus*)
        - Homalocephaloidea (*Homalocephale* + Pachycephalosaurus)
          - Homalocephalidae

            - Pachycephalosauridae
- Ceratopsia (*Triceratops* > *Pachycephalosaurus*)
    - Psittacosauridae
    - Neoceratopsia
        - Coronosauria
            - Protoceratopsidae
            - Bagaceratopidae
            - Ceratopsoidea
                - Leptoceratopsidae
                - Ceratopsomorpha
                    - Ceratopsidae

                        - Centrosaurine
                        - Chasmosaurie

Chapter- 7

Dinosaur Sculptures

Cabazon Dinosaurs

Cabazon Dinosaurs

Tourists can walk inside Dinny the Dinosaur

Coordinates	33°55′12.41″N 116°46′22.24″W / 33.9201139°N 116.7728444°W
Architectural style	Novelty architecture
Town	Cabazon, California
Country	United States
Started	1964 (Dinny) / 1981 (Mr. Rex)

Completed	1975 (Dinny) / 1986 (Mr. Rex)
Cost	$300,000 (Dinny)
Architect	Claude K. Bell
Structural engineer	Gerald Hufstetler

Cabazon Dinosaurs, also referred to as **Claude Bell's Dinosaurs**, are enormous, sculptured roadside attractions located in Cabazon, California and visible to the immediate north of Interstate 10. The site features **Dinny the Dinosaur**, a 150-ton building shaped like a larger-than-life-sized *Apatosaurus*, and **Mr. Rex**, a 100-ton *Tyrannosaurus rex* structure. Dinny (pronounced "Dine-ee") and Mr. Rex are at the Cabazon exit of Interstate 10 in California, a short distance west of Palm Springs behind the Wheel Inn diner on Seminole Drive in San Gorgonio Pass.

History

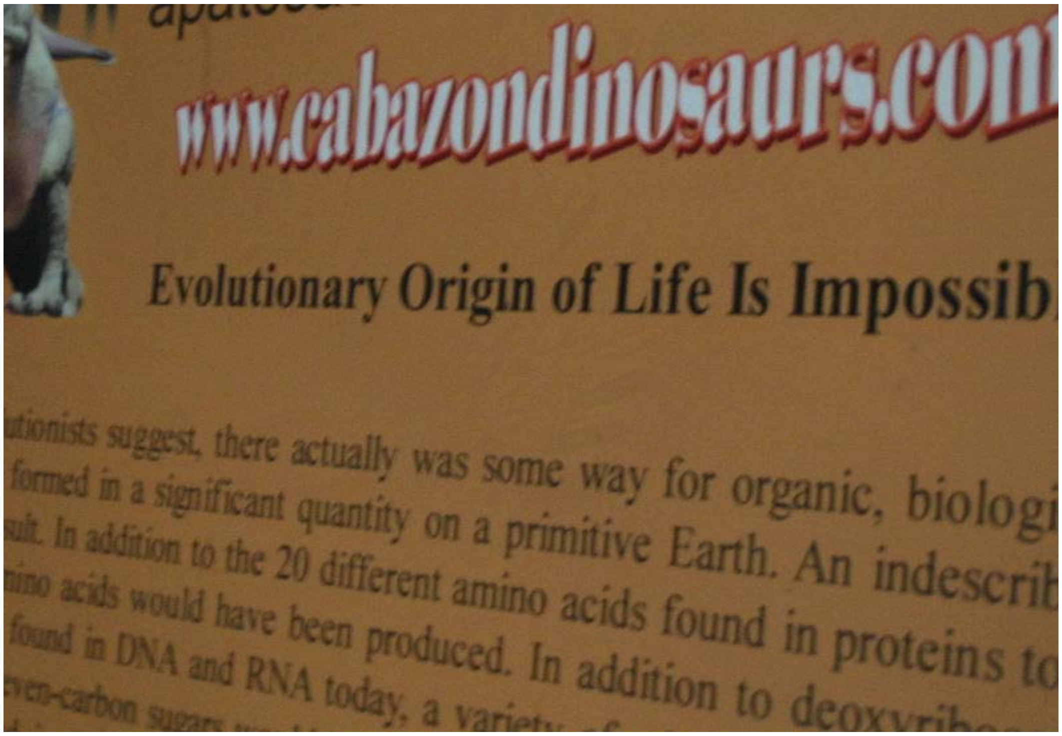
The Wheel Inn Restaurant, once owned by Claude Bell

The creation of the Cabazon dinosaurs began in the 1960s by Knott's Berry Farm sculptor and portrait artist Claude K. Bell (1897–1988) to attract customers to his Wheel Inn Cafe, which opened in 1958. Dinny, the first of the Cabazon dinosaurs, was started in 1964 and created over a span of eleven years. Bell created Dinny out of spare material salvaged from the construction of nearby Interstate 10 at a cost of $300,000. The biomorphic building that was to become Dinny was first erected as steel framework over which an expanded metal grid was formed in the shape of a dinosaur. All of it was then covered with coats of shotcrete (spray concrete). Bell was quoted in 1970 as saying the 45-foot

(14 m) high, 150-foot (46 m) long Dinny was "the first dinosaur in history, so far as I know, to be used as a building." His original vision for Dinny was for the dinosaur's eyes to glow and mouth to spit fire at night, predicting, "It'll scare the dickens out of a lot of people driving up over the pass." These two features, however, were not added. With the help of ironworker Gerald Hufstetler, Bell worked on the project independently; no construction companies or contractors were involved in the fabrication. The task of painting Dinny was completed by a friend of Bell's in exchange for one dollar and a case of Dr Pepper.

A second dinosaur, Mr. Rex, was constructed near Dinny in 1981. Originally, a giant slide was installed in Rex's tail; it was later filled in with concrete making the slide unusable. A third woolly mammoth sculpture and a prehistoric garden were drafted, but never completed due to Bell's death in 1988.

Creationist museum



tionists suggest, there actually was some way for organic, biologi
formed in a significant quantity on a primitive Earth. An indescrib
ult. In addition to the 20 different amino acids found in proteins to
nino acids would have been produced. In addition to deoxyribo
found in DNA and RNA today, a variety
ven-carbon sugars

Exhibits and displays inside Dinny detail arguments for Young Earth creationism and against evolutionism. This one concludes that the "Evolutionary Origin of Life Is Impossible."

Following the sale of the property by Bell's surviving family in the mid-1990s, Cabazon Family Partnership and MKA Cabazon Partnership of Costa Mesa, California became the new owners of the roadside attraction. The partnership obtained approval for a major expansion of the Cabazon dinosaur site in 1996 with the land-use approvals including restaurants, a museum, and gift shop, and a 60-room motel at the Main Street exit in Cabazon. Orange County developer and MKA partner Gary Kanter states the original vison has been for MKA to transform the area into a children's science and museum exhibit.

Currently located inside Dinny is a gift store and museum promoting creationism with some of the toy dinosaurs in the shop sold under the label "Don't swallow it! The fossil record does not support evolution." The current ownership has expressed a Young Earth creationist belief that most dinosaurs were created on Earth about 6,000 years ago - the same day as Adam and Eve. In stark contrast to that belief are Bell's painted frescoes and sculptures inside Dinny, depicting a naturalist and evolutionist viewpoint. Bell's paintings include representations of Cro-Magnon man (labeled "Cro-Magnon Man 30,000 [years ago]") and Java Man (labeled "Java Man 400,000"). Bell's historic displays now exist alongside information detailing the creationist viewpoint of the earth and man's origins.

The Cabazon Dinosaurs attraction also features an open-air museum with fiberglass and robotic dinosaurs. Other activities at the site include a sand pit where visitors can experience a "dino dig" as well as a gemstone and fossil panning sluice. Pastor Robert Chiles, assisting Kanter in turning the exhibit into a non-denominational church, has been quoted as to his belief of why children are drawn to the dinosaur attraction, "There's something in their DNA that knows man walked with these creatures on Earth." Chiles and Kanter plan to promote their views of creationism at the attraction based on their interpretation of the Book of Genesis.

Crystal Palace Dinosaurs

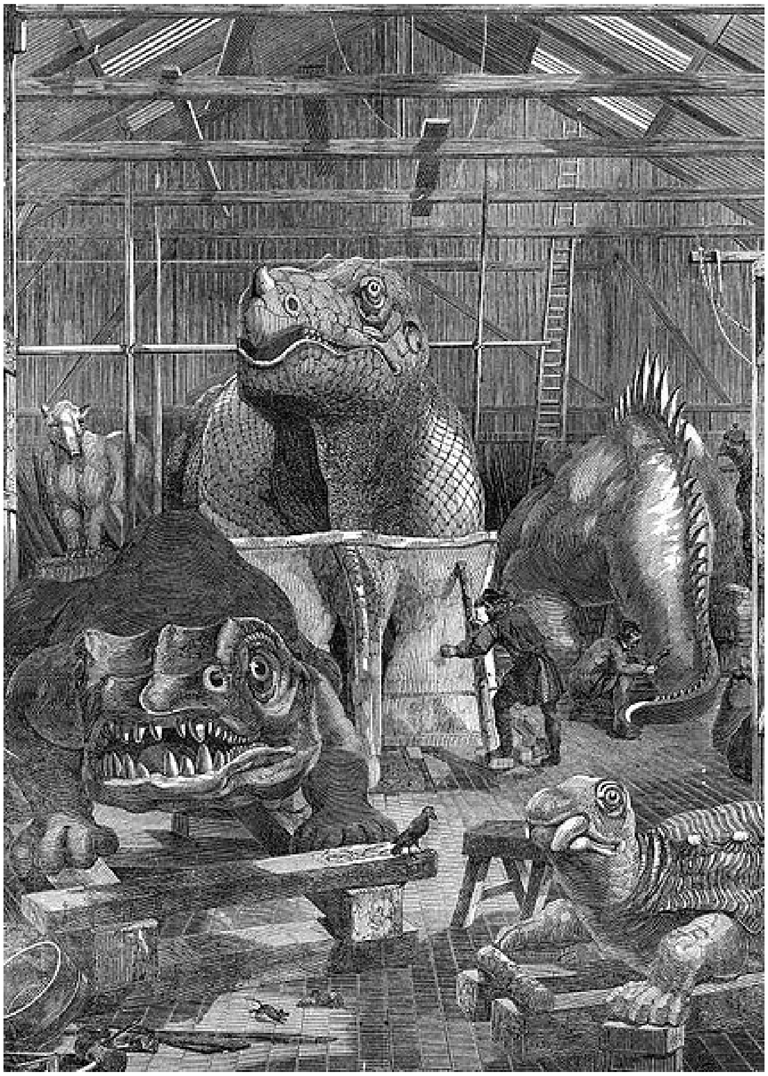
Overview of the dinosaur area of Crystal Palace

The **Crystal Palace Dinosaurs**, also known as **Dinosaur Court**, are a series of sculptures of dinosaurs and extinct mammals located in Crystal Palace, London.

Commissioned in 1852 and unveiled in 1854, they were the first dinosaur sculptures in the world, pre-dating the publication of Charles Darwin's *On the Origin of Species* by six years. Designed and sculpted by Benjamin Waterhouse Hawkins with the help of Richard Owen, they were Grade II listed buildings from 1973, extensively restored in 2002 and upgraded to Grade I listed in 2007.

The models themselves are now considered out of date and to varying degrees inaccurate.

History

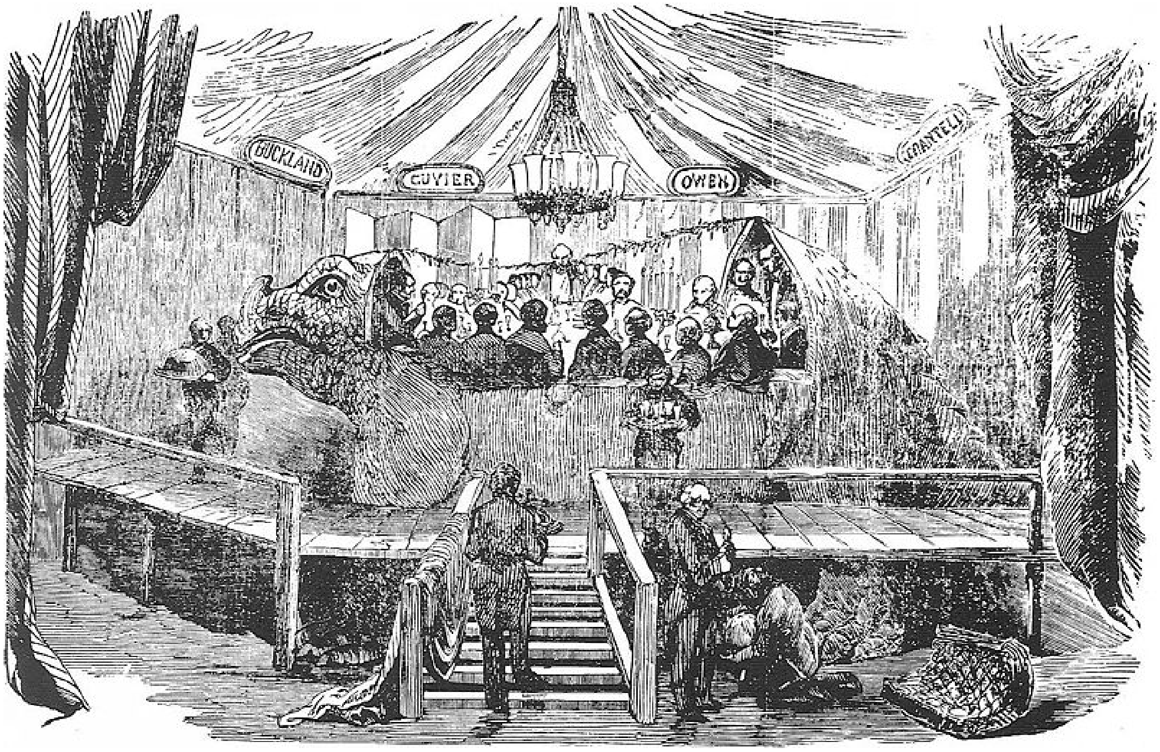


The dinosaur models under construction at Benjamin Waterhouse Hawkins' studio in Sydenham.

Following the closure of the Great Exhibition in October 1851, The Crystal Palace was bought and moved to Sydenham Hill, South London by the newly formed Crystal Palace Company; the grounds that surrounded it were then extensively renovated and turned into a public park with ornamental gardens, replicas of statues and two new man-made lakes.

As part of this renovation Benjamin Waterhouse Hawkins was commissioned to build the first ever life-sized models of extinct animals. He had originally planned to just re-create extinct mammals before deciding on building dinosaurs as well, which he did with advice from Sir Richard Owen, a celebrated biologist and palaeontologist of the time. Hawkins set up a workshop on site at the park and built the models there.

The models were displayed on three islands acting as a rough time-line, the first island representing roughly the Paleozoic era, a second representing the Mesozoic era, and a third representing the Cenozoic era. All of the mammals on the third island, however, were later moved to other locations on in the park (which in many ways directly led to them falling into ill-repair). The models' realism was aided by the lake at the time being 'tidal' and rising and falling, revealing different amounts of the dinosaurs. To mark the 'launch' of the models Hawkins held a dinner on New Year's Eve 1853 inside the mould of one of the *Iguanodon*.



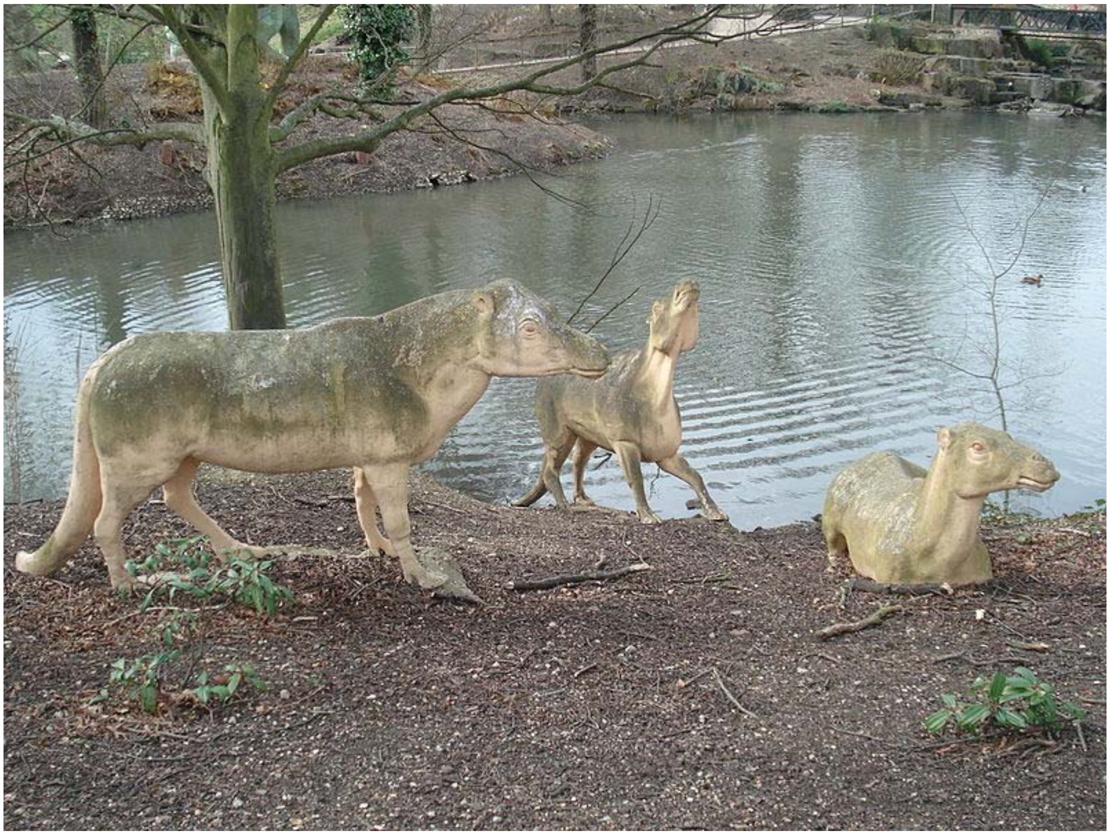
The famous banquet in the Crystal Palace *Iguanodon*, New Year's Eve 1853.

Hawkins benefited greatly from the public's reaction to them, which was so strong it led to what could be considered the first case of tie-in merchandising as a set of smaller versions of Hawkins's models were sold for £30 as educational products. But the building of the models was costly (having cost around £13,729) and in 1855 the Crystal Palace Company cut Hawkins's funding, leaving several planned models unmade or half finished and scrapped, despite protest from various sources including newspaper *The Observer*.

As further and fuller discoveries of the species included in Crystal Palace were made, the reputation of the models declined. By as early as 1895 experts looked on them with scorn and ridicule *The Crystal Palace Dinosaurs* by Steve McCarthy and Mick Gilbert quotes American fossil hunter Othniel Charles Marsh who scorns the dinosaurs' 'friends' as doing them a great injustice and speaks angrily of the models. The models and indeed the park fell into ill-repair as the years went by, a process aided by the fire that destroyed the Crystal Palace itself in 1936. The visibility of the models became obscured by overgrown foliage, but a full restoration of the animals was carried out in the 1950s by Victor H.C. Martin, this is when the animals were moved around.

Though general and often ad-hoc maintenance was carried up in the meantime (including the use of plasticine) the dinosaurs did not undergo a full restoration until 2002; during that time the park had fallen into total disarray and at one point a guided tour of the dinosaurs was the only time the park was open to the public. In 2002 the Institute of Historic Building Conservation totally renovated the models, including properly fixing and re-painting the existing models (in much lighter or at times totally different colors, for instance the *Megatheirium* was changed from blue to beige during the restoration). The institute also had fiberglass replacements created for the missing pterodactyls and their cliff, cutting away a lot of the foliage and restoring the original recreations of plant life that accompanied the models in the 1850s.

The sculptures



The *Anoplotherium* herd

The *Ichthyosaurus*

The *Iguanodon* sculptures

The *Megalosaurus* sculpture

Megaloceros sculptures

The two *Teleosaurus*

Fifteen species of extinct creatures currently reside in the park, as well as this at least three other genera (*Dinornis*, a mastodon, and *Glyptodon*s) were planned, and if contemporary reports are accurate at Hawkins began to build at least the mastodon before the Crystal Palace Company cut his funding in 1855. An inaccurate map of the time, reprinted in Steve McCarthy and Mick Gilbert's book *The Crystal Palace Dinosaurs*, even gives the planned locations of the *Dinornis* and mastodon.

The fifteen genera that were completed were:

Anoplotherium An extinct mammal: Hawkins's models draw very much on speculation about its camel-like appearance, and they resemble camels a great deal (it is now believed they look more like hippopotamus or pigs). Three models were originally made, but one, with its head raised, went missing in unknown circumstances but is now back with the other two on display.

Dicynodon Crystal Palace's *Dicynodon*, of which there are two, are based on fossils found in South Africa which were largely incomplete, as such the models are based heavily on turtles or tortoises complete with a shells and turtle stance. To date there is no evidence of any shelled *Dicynodon* and recent more complete fossils have revealed they looked more like Hippopotamus.

Hylaeosaurus Curiously, when their names are taken into consideration, it is *Hyleosaurus*, not *Iguanodon*, that most resembles the giant iguana stereotype of early ideas of dinosaurs. Today *Hylaeosaurus* is depicted similar to *Ankylosaurus*; Hawkins's depiction is of a large Iguana-like beast with long sharp spines along its back. The head of the *Hylaeosaurus* model is in fact not the original but a fiberglass replica; the original head is positioned outside the park's visitor's centre.

Ichthyosaurus Though a portion of the three *Ichthyosaurus* are submerged by water (though early shots show that unlike the *Mosasaurus* most of the model was completed) they are in fact basking on the land similar to Seals or Walrus do today, something we now know would kill them. In the time of the Crystal Palace Dinosaurs' productions the beasts were considered more along the lines of crocodiles or the *Plesiosaurus*; recently it has been uncovered they have more in common with sharks and dolphins with a dorsal fin and fish-like tail, both of which are not present in Hawkins's models. Instead the tails are a flat protuberance from a straight backbone. A further discrepancy is that the models' eyes have exposed sclerotic plates (bones that stopped their eyes from being crushed by the pressure under sea). However as a whole the ichthyosaurs are one of the more accurate animals and became one of the three 'mascot dinosaurs' along with the *Iguanodon* and *Megalosaurus* (although ichthyosaurs are not dinosaurs at all).

Iguanodon Easily the most recognizable and most commonly shown of Hawkins's models are the pair of *Iguanodon*. The inaccuracy of having thumb spikes mistaken for horns is used repeatedly on documentaries about dinosaurs and their history when talking about Victorian ideas of the beasts. Aside from this the *Iguanodon*, like the

Megalosaurus, were depicted as quadrupeds (walking on all fours) and look as though they are inspired by modern day dogs.

Labyrinthodon Three *Labyrinthodon* models were made for Crystal Palace, heavily based on frogs. One is smooth skinned and is based on the species *Labyrinthodon salamandroides*. Two were based on *Labyrinthodon pachygnathus* (both have since been re-classified). Casts of the animal's real footprints were included in the ground around the models (one of which had survived by the time of *The Crystal Palace Dinosaurs* being written).

Megaloceros Hawkins built a whole family unit of male, female and fawn; the adults bore antlers made from actual fossil antlers, though these have since been replaced. Moved from the third island, they had fallen into disrepair as they were in a place easily accessible by vandals. Until their antlers were replaced, the Elks were the most accurate of the models, though given that they are only large deer and stag anyway, there was much more reference for them in 1852.

Megalosaurus Giant and visually impressive even by today's standards, the *Megalosaurus* became one of the park's three 'mascot dinosaurs' along with the *Iguanodon* and (less so) the Ichthyosaurs. Yet it is arguably the most inaccurate of all of Hawkins's models, depicted as a quadruped that looks like an elephant with a lizard's head and paws.

Megatherium Wholly more accurate than most of the dinosaur species, the *Megatherium* was part of the park's children's zoo for many years with its tail in the goats and guinea pigs enclosure. Once the zoo was closed, it became totally inaccessible, only to be seen through the railings that kept visitors out of the derelict area. Recent renovations demolished the zoo and a walkway has caused the *Megatherium* to become one of the models visitors can now get the closest to.

Mosasaurus At the time of the models being built, only skulls of *Mosasaurus* had been discovered. In a clever way of disguising this lack of information, Hawkins only built the head and back of the animal. He submerged the model deep in the lake so the water hid this fact, leaving little room for inaccuracy. Despite this it does look noticeably different from modern reconstructions of the beast. The *Mosasaurus* at Crystal Palace is positioned in an odd place near the secondary island that was originally a waterfall, and much of it is obscured if viewed from the lakeside path.

Palaeotherium The herd of *Palaeotherium*, an extinct tapir-like mammal, have suffered the most ill-repair of all of the models, and the standing model looked very little like the original model by Hawkins; prior to the 2002 restoration they were in such bad shape they were removed totally and were stored with miscellaneous equipment. They have since been restored and put back on show but still show surface wearing. Some sources state that these models were added at a later date but a *London News* illustration of Hawkins's workshop clearly shows them in the background, appearing to prove these sources inaccurate.

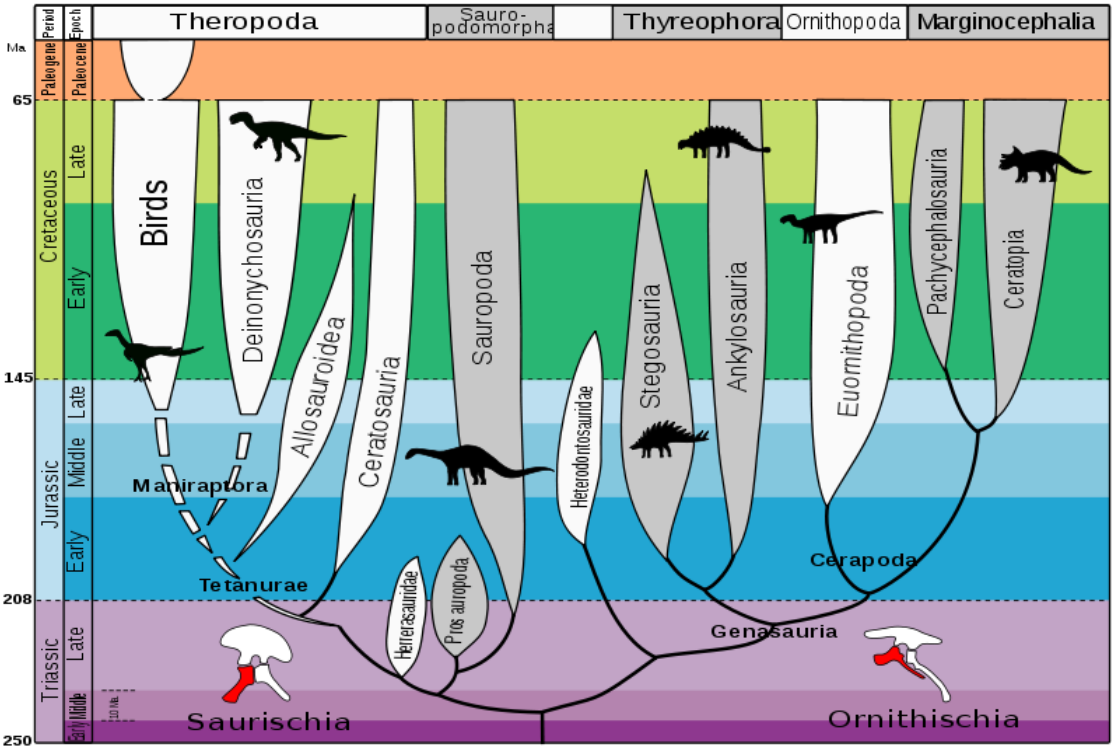
Plesiosaurus Each of the three plesiosaur models are intended to represent a different genus, and generally are fairly accurate to today's standards with the exception of two models' incredibly flexible necks, which twist in nearly impossible ways.

Pterodactyl The most common way of someone drawing a pterodactyl is to give the animal a head with an additional point, making its head almost symmetrical to its beak, but there were species of *Pteranodon* that had simple bald heads devoid of these points. Hawkins's pterodactyls are some of his more accurate models (again despite their pipe-cleaner style necks). At some point the two models that stood beside the *Iguanodon* on the central island went missing; they have since been restored in the recent 2002 renovations.

Teleosaurus Arguably Hawkins's most accurate model, the two Teleosaurs are depicted virtually the same as they are today (thin crocodiles with very long thin jaws and small eyes).

Chapter- 8

Evolution of Dinosaurs



Evolution of dinosaurs

Dinosaurs evolved from the archosaurs 232-234 Ma (million years ago) in the Ladinian age, the latter part of the middle Triassic. Dinosauria is a well-supported clade, present in 98% of bootstraps. It is diagnosed by many features including loss of the postfrontal on the skull and an elongate deltopectoral crest on the humerus.

From archosaurs to dinosaurs

The process leading up the first dinosaurs can be followed through fossils of the early Archosaurs such as the Proterosuchidae, *Erythrosuchidae* and *Euparkeria* which have fossils dating back to 250 Ma, through mid-Triassic archosaurs such as *Ticinosuchus* 232-236 Ma. Crocodiles are also descendants of mid-Triassic archosaurs.

The dinosaurs can be defined as the last common ancestor of birds (Saurischia) and *Triceratops* (Ornithischia) and all the descendants of that ancestor. With that definition, the pterosaurs and several species of archosaurs narrowly miss out on being classed as dinosaurs. The pterosaurs are famous for flying through the Mesozoic skies on leathery wings. Archosaur genera that narrowly miss out on being classified as dinosaurs include *Schleromochlus* 220-225 Ma, *Lagerpeton* 230-232 Ma and *Marasuchus* 230-232 Ma.

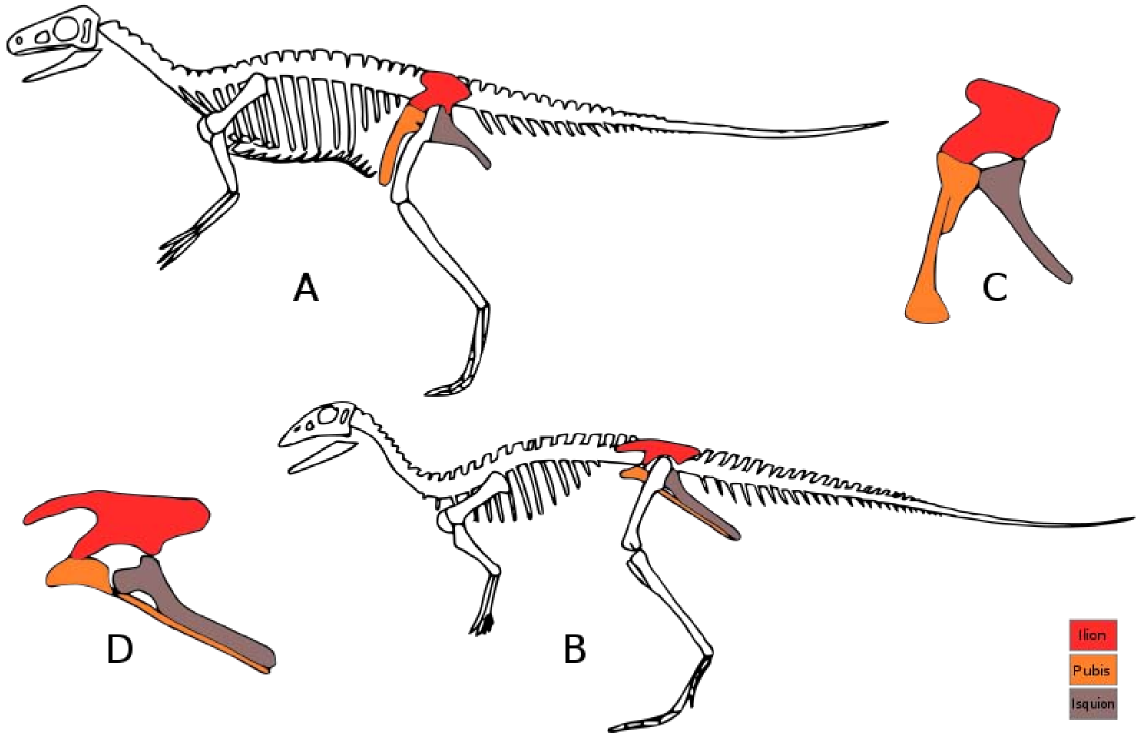
Earliest dinosaurs

The first known dinosaurs were bipedal predators that were one to two metres long.

Spondylosoma may or may not be a dinosaur; the fossils (all postcranial) are tentatively dated at 230-232 Ma.

The earliest confirmed dinosaur fossils include saurischian ('lizard-hipped') dinosaurs *Saturnalia* 225-232 Ma, *Herrerasaurus* 220-230 Ma, *Staurikosaurus* possibly 225-230 Ma, *Eoraptor* 220-230 Ma and *Alwalkeria* 220-230 Ma. *Saturnalia* may be a basal saurischian or a prosauropod. The others are basal saurischians.

Among the earliest ornithischian ('bird-hipped') dinosaurs is *Pisanosaurus* 220-230 Ma. Although *Lesothosaurus* comes from 195-206 Ma, skeletal features suggest that it branched from the main Ornithischia line at least as early as *Pisanosaurus*.



A. *Eoraptor*, an early saurischian, **B** *Lesothosaurus*, a primitive ornithischian, **C** *Staurikosaurus* (Saurischia) pelvis, **D** *Lesothosaurus* pelvis

It is clear from this figure that early saurischians resembled early ornithischians, but not modern crocodiles. Saurischians are distinguished from the ornithischians by retaining the ancestral configuration of bones in the pelvis. Another difference is in the skull, the upper skull of the Ornithischia is more solid and the joint connecting the lower jaw is more flexible; both are adaptations to herbivory and both can already be seen in *Lesothosaurus*.

Saurischia

Setting aside the basal Saurischia, the rest of the Saurischia are split into the Sauropodomorpha and Theropoda. The Sauropodomorpha is split into Prosauropoda and Sauropoda. The evolutionary paths taken by the Theropoda are very complicated. *The Dinosauria* (2004), a major reference work on dinosaurs, splits the Theropoda into groups Ceratosauria, Basal Tetanurae, Tyrannosauroidea, Ornithomimosauria, Therizinosauroidea, Oviraptorosauria, Troodontidae, Dromaeosauridae and Basal Avialae in turn. Each group branches off the main trunk at a later date.

Sauropodomorpha

The first sauropodomorphs were prosauropods. Prosauropod fossils are known from the late Triassic to early Jurassic 227-180 Ma. They could be bipedal or quadrupedal and had developed long necks and tails and relatively small heads. They had lengths of 2.5 to

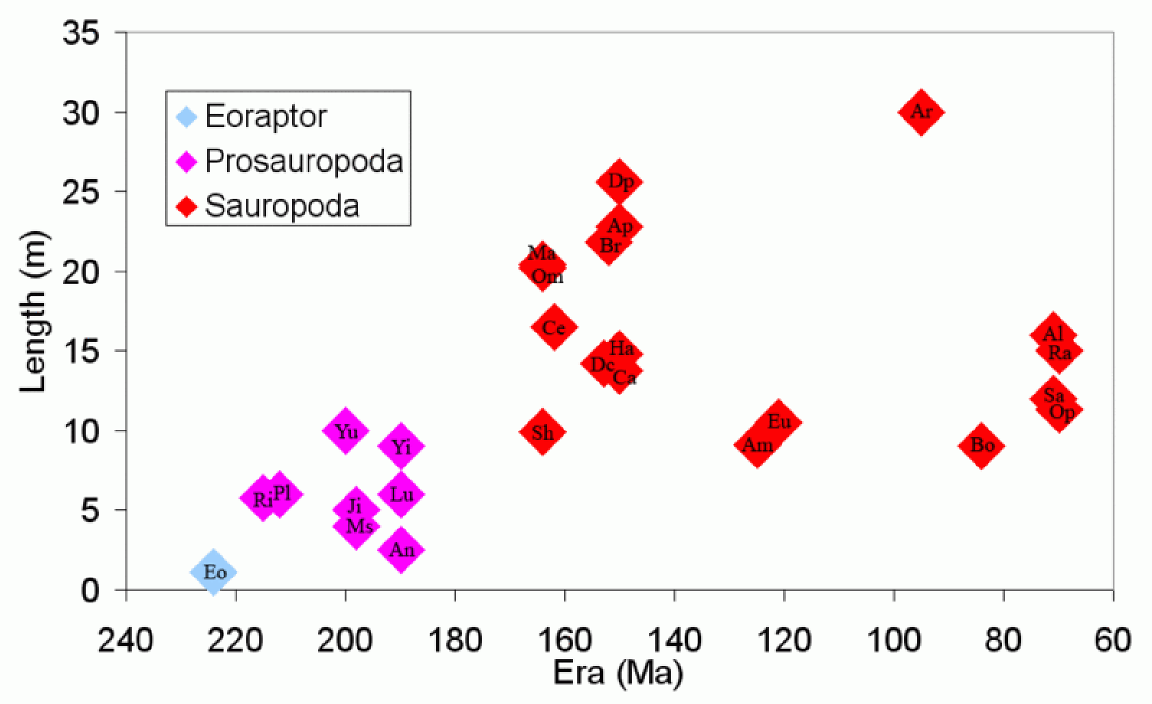
10 m and were primarily herbivorous. The earliest prosauropods, such as *Thecodontosaurus* from 205-220 Ma, still retained the ancestral bipedal stance and large head to body ratio.

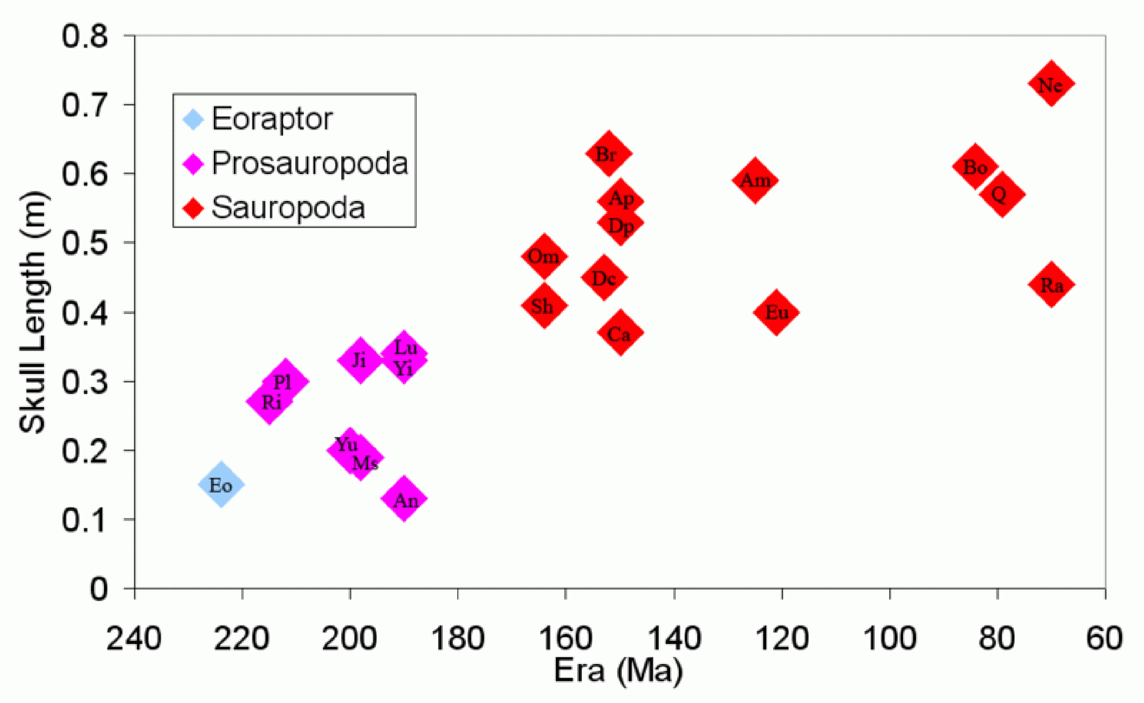
These evolved into the sauropods which became gigantic quadrupedal herbivores, some of which reached lengths of at least 26 m. Features defining this clade include a forelimb length to hindlimb length greater than 0.6. Most sauropods still had hindlimbs larger than forelimbs; one notable exception is *Brachiosaurus* whose long forelimbs suggest that it had evolved to feed from tall trees like a modern-day giraffe.

Sauropod fossils are found from the times of the earliest dinosaurs right up to the K-T extinction event, from 227 to 65 Ma. Most sauropods are known from the Jurassic, to be more precise between 227 and 121 Ma.

The Cretaceous sauropods form two groups. The Diplodocoidea lived from 121 to 65 Ma. The Titanosauriformes lived from 132 to 65 Ma. The latter clade consists of series of nested subgoups, the Titanosauria, the Titanosauridae and Saltasauridae. Both the Diplodocoidea and Titanosauriformes are descended from the Neosauropoda, the earliest of which lived in about 169 Ma.

The sauropods are famous for being the largest land animals that ever lived, and for having relatively small skulls. The enlargement of prosauropod and sauropod dinosaurs into these giants and the change in skull length is illustrated in the following charts.





Dinosaurs used in creating these charts are (in date order): Eo *Eoraptor*; Prosauropods Ri *Riojasaurus*, Pl *Plateosaurus*, Yu *Yunnanosaurus*, Ms *Massospondylus*, Ji *Jingshanosaurus*, An *Anchisaurus*, Lu *Lufengosaurus*, Yi *Yimenosaurus*, ; and Sauropods Sh *Shunosaurus*, Om *Omeisaurus*, Mm *Mamenchisaurus*, Ce *Cetiosaurus*, Dc *Dicraeosaurus*, Br *Brachiosaurus*, Eu *Euhelopus*, Ap *Apatosaurus*, Ca *Camarasaurus*, Dp *Diplodocus*, Ha *Haplocanthosaurus*, Am *Amargasaurus*, Ar *Argentinosaurus (approx)*, Bo *Bonitasaura*, Q *Quaesitosaurus*, Al *Alamosaurus*, Sa *Saltasaurus*, Ra *Rapetosaurus*, Op *Opisthocoelicaudia*, Ne *Nemegtosaurus*.

With the exception of *Argentinosaurus* (included to fill a gap in time), these graphs show only the length of sauropods for whom near-complete fossil skeletons are known. It doesn't show other very large sauropods because these are only known from very incomplete skeletons. The ratio of skull length to body length is much higher in *Eoraptor* than in sauropods. The longest skull graphed is of *Nemegtosaurus*, which is not thought be a particularly large sauropod. The skull of *Nemegtosaurus* was found near the headless skeleton of 11 metre long *Opisthocoelicaudia*, and it has been suggested that they may be the same species, but see Nemegtosauridae.

The relationship between the evolution of large herbivores and large plants remains uncertain. About 50% of the plants over the time of the dinosaurs were conifers, they increased in number in the Triassic until stabilising in about 190 Ma. Cycads formed the second largest group until about 120 Ma. Ferns were present in roughly constant numbers the whole time. Flowering plants began about 120 Ma and by the end of the period had taken over from the cycads. All dinosaur herbivores appear to have been adversely affected by the extinction event at the end of the Jurassic.

Theropoda

By far the earliest fossils of Theropoda (not counting the basal saurischians) are of the Coelophysoidea, including *Coelophysis* and others, from late Triassic and early Jurassic 227-180 Ma. Cladistic analysis sometimes connects these to the group called Ceratosauria. Principal features of both include changes in the pelvic girdle and hind limb that differ between the sexes. Other ceratosauria first appear in the late Jurassic of western North America.

These are followed by the basal Tetanurae, of whom fossils have been found from the mid Jurassic to past the end of the early Cretaceous 180 Ma to 94 Ma. They have a relatively short maxillary tooth row. They did not all branch off the evolutionary line leading to coelurosaurs at the same time. Basal tetanurans include Megalosauridae, spinosaurids, a diverse clade of allosaurs, and several genera of less certain affinities, including *Compsognathus*. With the exception of *Compsognathus* they are large-bodied. Allosaurs form a distinct long-lived clade that share some cranial characters. They include the well known *Allosaurus* and *Sinraptor* among others.

The great radiation of Theropoda into many different clades of Coelurosauria must have happened in the mid to late Jurassic, because *Archaeopteryx* was around in about 152-154 Ma, and cladistic analysis has shown that many other groups of Coelurosauria branched off before that. Fossil evidence from China suggests that the earliest feathers were found on the primitive Coelurosauria. The most primitive of these, e.g. on the tyrannosauroid *Dilong*, were simply hollow-cored fibres that would have been useful for insulation but useless for flying.

Occasional bones and cladistic analyses point to the Tyrannosauroidea branching off from the other Theropoda early, in the middle Jurassic, although nearly complete skeletons haven't yet appeared before *Eotyrannus* from 121-127 Ma, and the many close relatives of *Tyrannosaurus* itself don't appear before 84 Ma, near the end of the late Cretaceous.

Ornithomimosauria fossils are known from 127 to 65 Ma. The earliest branch from the main line of Ornithomimosauria is believed to be *Harpymimus*.

The Therizinosauroidea are unusual theropods in being almost all vegetarian. Fossil Therizinosauroidea are known from 127 to 65 Ma.

Maniraptorans include Oviraptorosauria, Deinonychosaurs and birds. They are characterized by an ulna with a curved shaft.

Oviraptorosaurian fossils are known from 127 to 65 Ma. They have a toothless skull that is extremely modified. The skeleton has an unusually short tail.

Deinonychosaurs, named after the enlarged sickle-shaped second digit of the hand, are closely related to birds. They have two distinct families, Troodontidae and

Dromaeosauridae. Troodontid fossils are known from 127 to 65 Ma. They have the more slender build, and longer limbs. The earliest named troodontid fossil known is *Sinornithoides*. Dromaeosaurid fossils are known from about 127 to 65 Ma with the exception of *Utahraptor*. The skeletal remains of *Utahraptor* are about 127-144 Ma. This is interesting because according to a recent cladistic analysis, *Utahraptor* is about as far from the ancestral Theropoda as it is possible to get, further than *Archaeopteryx*. Dromaeosaurids have a larger second digit; this family includes the well known dinosaurs *Dromaeosaurus*, *Deinonychus* and *Velociraptor*.

Ancient birds (Avialae) include both the Aves, which are defined as descendants of the common ancestor of modern birds and *Archaeopteryx*, and the more primitive *Epidendrosaurus*. Fossil birds stretch down from 154 Ma through the K-T extinction event at 65 Ma to the present day. Scores of complete skeletons have now been found of the more recent *Confuciusornis*, which is an early representative of the Ornithurae. Ornithurans all have a bony pygostyle, to which tail feathers are anchored.

Ornithischia

Ornithischia, as the name indicates, was coined for the birdlike pelvic girdle, although they are not the ancestors of birds.

The ornithischian skull and dentition was modified very early by a herbivorous diet. *Lesothosaurus* separated early, but the skull of *Lesothosaurus* already shows such adaptations, with broad proportions, a less flexible upper jaw, and a more mobile connection for the lower jaw.

The major clades were already established by the early Jurassic. The ornithischians divided into armoured thyreophorans and unarmoured ornithopods and marginocephalians.

Thyreophorans

Surface body armour (scutes) is the most striking feature of the thyreophorans. *Scutellosaurus* has these but otherwise differs little from *Lesothosaurus*. It has a long tail and combined bipedal-quadrupedal posture that separates it from all later thyreophorans including Stegosauria and Ankylosauria. These two clades, although quite different in overall appearance, share many unusual features in the skull and skeleton.

Stegosaurs are easily recognised by the prominent row of plates above the spine and ling spines on the tail. Most stegosaurs, but not *Stegosaurus*, also have a spine over each shoulder. These spines and plates have evolved from the earlier surface scutes. *Huayangosaurus* is the oldest and most primitive known stegosaur.

Ankylosaurs are easily recognised by their extensive body armour. The skull is heavily ossified. Early in their evolution, ankylosaurs split into the Nodosauridae and Ankylosauridae, distinguished by features of the skull.

Ornithopoda

Ornithopods fall into one of three distinct clades - Heterodontosauridae, Hypsilophodontidae, and Iguanodontia.

Heterodontosaurids are very small (body length < 1 m) and lived in the early to late Jurassic. Apart from *Abrictosaurus* all have a short upper canine and longer lower canine. The forelimbs in known fossils are unusually long.

Hypsilophodontids more closely resemble their ancestors than the heterodontosaurids do. The most distinctive features are short scapula and rod-shaped pre-pubic process. The earliest is *Agilisaurus* from the middle Jurassic of China.

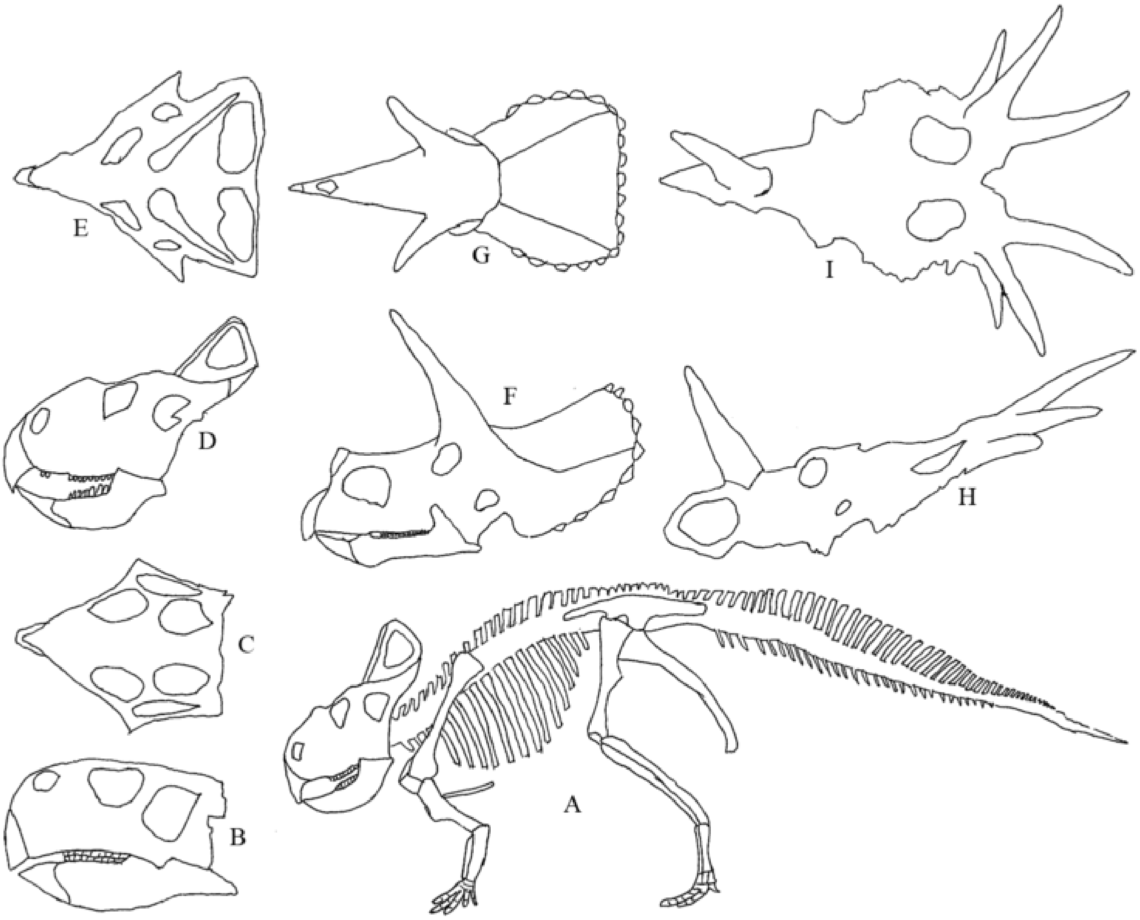
Iguanodontians are a diverse but morphologically tight knit array of genera known from fossils of the late Cretaceous. Significant modifications include the evolution of tooth batteries, a ligament-bound metacarpus and a digitigrade hand posture. *Tenontosaurus* is the most basal iguanodontian. Others include *Iguanodon*, *Camptosaurus* and *Muttaburrasaurus*.

Marginocephalia

Marginocephalia are named for a shelf that projects over the back of the skull. They include the pachycephalosaurians and ceratopsians.

Pachycephalosaurs are best known for their thick upper fronts to their skull. The oldest known is *Stenopelix*, from the early Cretaceous of Europe.

Ceratopsians, famous for *Protoceratops*, *Triceratops* and *Styracosaurus* illustrate the evolution of frilled and horned skulls. The frills evolved from the shelf common to all Marginocephalia. Ceratopsians are separated into basal ceratopsians, including the parrot-beaked *Psittacosaurus*, and neoceratopsians.



Diversity of ceratopsian skulls. A) Skeleton of *Protoceratops*. B) to I) Skulls. B) & C) *Psittacosaurus* side & top. D) & E) *Protoceratops* side & top. F) & G) *Triceratops* side & top. H) & I) *Styracosaurus* side (without lower jaw) & top.

The sequence of ceratopsian evolution in the Cretaceous is roughly from *Psittacosaurus* (121 -99 Ma) to *Protoceratops* (83 Ma) to (*Triceratops* 67 Ma and *Styracosaurus* 72 Ma). In side view the skull of *Psittacosaurus* bears very little resemblance to that of *Styracosaurus* but in top view a similar pentagonal arrangement can be seen.

Fossil record

The first few lines of primitive dinosaurs diversified rapidly through the Triassic period; dinosaur species quickly evolved the specialised features and range of sizes needed to exploit nearly every terrestrial ecological niche. During the period of dinosaur predominance, which encompassed the ensuing Jurassic and Cretaceous periods, nearly every known land animal larger than 1 meter in length was a dinosaur.

One measure of the quality of the fossil record is obtained by comparing the date of first appearance with the order of branching of a cladogram based on the shape of fossil elements. Close correspondence exists for ornithiscians, saurischians and subgroups. The cladogram link between coelophysids and ceratosaurs is an exception, it would place the origin of coelophysids much too late. The simplest explanation is convergent evolution - ceratosaur bones evolved independently into a shape that resembles that of the earlier coelophysids. The other possibility is that ceratosaurs evolved much earlier than the fossil record suggests.

Most dinosaur fossils have been found in the Norian-Sinemurian, Kimmeridgian-Tithonian, and Campanian-Maastrichtian periods. Continuity of lineages across the intervening gaps shows that those gaps are artifacts of preservation rather than any reduction in diversity or abundance.

In many instances, cladistic analysis shows that ancestral lineages of varying durations fall in those gaps. The length of missing ancestral lineages in 1997 range from 25 Ma (*Lesothosaurus*, Genasauria, Hadrosauroidea, Sauropoda, Neoceratopsia, Coelurosauria) to 85 Ma (Carcharodontosauridae). Because the dinosaurian radiation began at small body size, the unrecorded early history may be due to less reliable fossilization of smaller species. However, some missing lineages, notably of Carcharodontosauridae and Abelisauridae, require alternative explanations because the missing range extends across stages rich in fossil material.

Evolutionary trends

Body size

Body size is important because of its correlation with metabolism, diet, life history, geographic range and extinction rate. The modal body mass of dinosaurs lies between 1 and 10 tons throughout the Mesozoic and across all major continental regions. That said, there was a trend towards increasing body size within many dinosaur clades, including the Thyreophora, Ornithopoda, Pachycephalosauria, Ceratopsia, Sauropomorpha, and basal Theropoda. Marked decreases in body size have also occurred in some lineages, but are more sporadic. The best known example is the decrease in body size leading up to the first birds; *Archaeopteryx* was below 10 kg in weight, and later aves *Confuciusornis* and *Sinornis* are starling- to pigeon-sized.

Mobility

The ancestral dinosaur was a biped. The evolution of a quadrupedal posture occurred four times, among the ancestors of Euornithopoda, Thyreophora, Ceratopsia and Sauropodomorpha. In all four cases this was associated with an increase in body size, and in all four cases the trend is unidirectional without reversal.

Dinosaurs exhibit a pattern of the reduction and loss of fingers on the lateral side of the hand (digits III, IV and V). The primitive function of the dinosaur hand is grasping with a partially opposable thumb, rather than weight-bearing.

Effect of food sources

The ancestral dinosaur was a carnivore. Herbivory among dinosaurs arose three times, at the origin of the ornithischian, sauropodomorph, and therizinosaurid clades. Individual therizinosaurids are herbivorous or omnivorous. Herbivory among the ornithischians and sauropodomorphs was never reversed.

The potential co-evolution of plants and herbivorous dinosaurs has been subject to extensive speculation. The appearance of prosauropods in the late Triassic has been tentatively linked either to the demise or diversification of types of flora at that time. The rise of ceratopsids and iguanodont and hadrosaurid ornithopods in the Cretaceous has been tentatively linked to the angiosperm radiation. Unfortunately, there are still no hard data on dietary preferences of herbivorous dinosaurs, apart from data on chewing technique and gastroliths.

Biogeography

Dinosaurian faunas, which were relatively uniform in character when Pangaea began to break up, became markedly differentiated by the close of the Cretaceous. Biogeography is based on the splitting of an ancestral species by the emplacement of a geographic barrier. Interpretation is limited by a lack of fossil evidence for eastern North America, Madagascar, India, Antarctica and Australia. No unequivocal proof of the biogeographical action on Dinosaur species has been obtained, but some authors have outlined centres of origin for many dinosaur groups, multiple dispersal routes, and intervals of geographic isolation.

Dinosaurs that have been given as evidence of biogeography include abelisaurid theropods from South America and possibly else where on Gondwana.

Relationships between dinosaurs show abundant evidence of dispersal from one region of the globe to another. Tetanuran theropods travelled widely through western North America, Asia, South America, Africa and Antarctica. Pachycephalosaurs and ceratopsians show clear evidence of multiple bidirectional dispersion events across Beringa.

Extinction

The Cretaceous–Tertiary extinction event, which occurred 65.5 million years ago at the end of the Cretaceous period, caused the extinction of all dinosaurs except for the line that had already given rise to the first birds.

Chapter- 9

Physiology of Dinosaurs

The **physiology of dinosaurs** has historically been a controversial subject, particularly thermoregulation. Recently, many new lines of evidence have been brought to bear on dinosaur physiology generally, including not only metabolic systems and thermoregulation, but on respiratory and cardiovascular systems as well.

During the early years of dinosaur paleontology, it was widely considered that they were sluggish, cumbersome, and sprawling cold-blooded lizards. However, with the discovery of much more complete skeletons in the western United States, starting in the 1870s, scientists could make more informed interpretations of dinosaur biology and physiology. Edward Drinker Cope, opponent of Othniel Charles Marsh in the Bone Wars, propounded at least some dinosaurs as active and agile, as seen in the painting of two fighting "Laelaps" produced under his direction by Charles R. Knight. In parallel, the development of Darwinian evolution, and the discoveries of *Archaeopteryx* and *Compsognathus*, led Thomas Henry Huxley to propose that dinosaurs were closely related to birds. Despite these considerations, the image of dinosaurs as large reptiles had taken root, and most aspects of their paleobiology were interpreted as being typically reptilian for the first half of the twentieth century. Beginning in the 1960s and with the advent of the Dinosaur Renaissance, views of dinosaurs and the physiology have changed dramatically, including the discovery of feathered dinosaurs in Early Cretaceous age deposits in China, indicating that birds evolved from highly agile maniraptoran dinosaurs.

History of study

Early interpretations of dinosaurs: 1820s to early 1900s

The study of dinosaurs began in the 1820s in England. Pioneers in the field, such as William Buckland, Gideon Mantell, and Richard Owen, interpreted the first, very fragmentary remains as belonging to large quadrupedal beasts. Their early work can be seen today in the Crystal Palace Dinosaurs, constructed in the 1850s and which present known dinosaurs as elephantine lizard-like reptiles. Despite these reptilian appearances, Owen speculated that dinosaur heart and respiratory systems were more mammal-like than reptile-like.

The 1897 painting of "*Laelaps*" (now *Dryptosaurus*) by Charles R. Knight.

Changing views and the Dinosaur Renaissance

However, in the late 1960s views began to change, beginning with John Ostrom's work on *Deinonychus* and bird evolution. His student, Bob Bakker, popularized the changing thought in a series of papers beginning with *The superiority of dinosaurs* in 1968. In these publications, he argued strenuously that dinosaurs were warm-blooded and active animals, capable of sustained periods of high activity. In most of his writings Bakker framed his arguments as new evidence leading to a revival of ideas popular the late 19th century, frequently referring to an ongoing *dinosaur renaissance*. He used a variety of anatomical and statistical arguments to defend his case, the methodology of which was fiercely debated among scientists.

These debates sparked interest in new methods for ascertaining the palaeobiology of extinct animals, such as bone histology, which have been successfully applied to determining the growth-rates of many dinosaurs.

Today, it is generally thought that many or perhaps all dinosaurs had higher metabolic rates than living reptiles, but also that the situation is more complex and varied than Bakker originally proposed. For example, while smaller dinosaurs may have been true endotherms, the larger forms could have been inertial homeotherms, or many dinosaurs could have had intermediate metabolic rates.

Feeding and digestion

The earliest dinosaurs were almost certainly predators, and shared several predatory features with their nearest non-dinosaur relatives like *Lagosuchus*, including: relatively large, curved, blade-like teeth in large, wide-opening jaws that closed like scissors; relatively small abdomens, as carnivores do not require large digestive systems. Later dinosaurs which are regarded as predators sometimes grew much larger, but retain the same set of features. Instead of chewing their food, these predators swallowed it whole.

The feeding habits of ornithomimosaurs and oviraptorosaurs are a mystery: although they evolved from a predatory theropod lineage, they have small jaws and lack the blade-like teeth of typical predators, but there is no evidence of their diet or how they ate and digested it.

Features of other groups of dinosaurs indicate that they were vegetarians: jaws that opened to only a small extent and closed more like shutters, so that all the teeth met at the same time; large abdomens to accommodate the large amounts of vegetation they ate and store this food for a longer time, as vegetation is harder to digest than meat; these large digestive systems may also have contained endosymbiotic micro-organisms which can digest cellulose, as no known animal can digest this tough material directly.

Sauropods, which were vegetarians, did not chew their food, as their teeth and jaws appear suitable only for stripping leaves off plants. Ornithischians, also vegetarians, show a variety of approaches. The armored ankylosaurs and stegosaurs had small heads and weak jaws and teeth, and are thought to have fed in much the same way as sauropods. The pachycephalosaurs had small heads and weak jaws and teeth, but their lack of large digestive systems suggests a different diet, possibly fruits, seeds, or young shoots, which would have been more nutritious than leaves.

On the other hand ornithopods such as *Hypsilophodon*, *Iguanodon* and various hadrosaurs had horny beaks for snipping off vegetation and jaws and teeth that were well-adapted for chewing. The horned ceratopsians had similar mechanisms.

It has often been suggested that at least some dinosaurs used swallowed stones, known as gastroliths, to aid digestion by grinding their food in muscular gizzards, and that this was a feature they shared with birds. In 2007 Oliver Wings reviewed references to gastroliths in scientific literature and found considerable confusion, starting with the lack of an agreed and objective definition of "gastrolith". He found that swallowed hard stones or grit can assist digestion in birds that were mainly feeding on grain but may not be essential, and that birds which eat insects in summer and grain in winter usually get rid of the stones and grit in summer. Gastroliths have often been described as important for sauropod dinosaurs, whose diet of vegetation required very thorough digestion, but Wings concluded that this idea was incorrect: gastroliths are found with only a small percentage of sauropod fossils; where they have been found, the amounts are too small and in many cases the stones are too soft to have been effective in grinding food; most of these gastroliths are highly polished, but gastroliths used by modern animals to grind food are roughened by wear and corroded by stomach acids; hence the sauropod gastroliths were probably swallowed accidentally. On the other hand he concluded that gastroliths found with fossils of advanced theropod dinosaurs such as *Sinornithomimus* and *Caudipteryx* resemble those of birds, and that the use of gastroliths for grinding food may have appeared early in the group of dinosaurs from which these dinosaurs and birds both evolved.

Reproductive biology

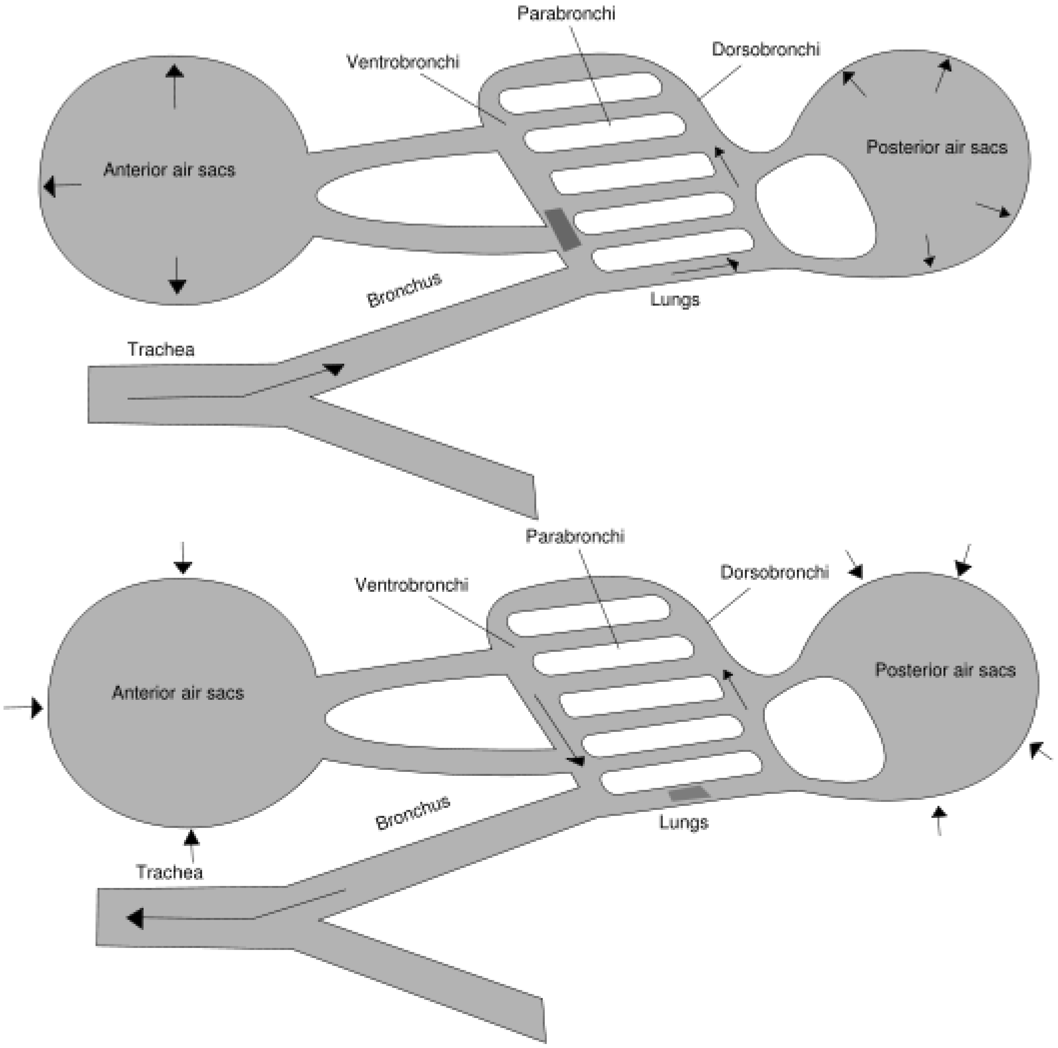
When laying eggs, females of some bird species grow a special type of bone in their limbs between the hard outer bone and the marrow. This medullary bone, which is rich in calcium, is used to make eggshells, and the birds which produced it absorb it when they have finished laying eggs. Medullary bone has been found in fossils of the theropods *Tyrannosaurus* and *Allosaurus* and of the ornithopod *Tenontosaurus*.

Because the line of dinosaurs that includes *Allosaurus* and *Tyrannosaurus* diverged from the line that led to *Tenontosaurus* very early in the evolution of dinosaurs, the presence of medullary bone in both groups suggests that dinosaurs in general produced medullary tissue. On the other hand crocodilians, which are dinosaurs' second closest living relatives after birds, do not produce medullary bone. This tissue may have first appeared in ornithodires, the Triassic archosaur group from which dinosaurs are thought to have evolved.

Medullary bone has been found in specimens of sub-adult size, which suggests that dinosaurs reached sexual maturity before they were fully-grown. Sexual maturity at sub-adult size is also found in reptiles and in medium- to large-sized mammals, but birds and small mammals reach sexual maturity only after they are fully-grown – which happens within their first year. Early sexual maturity is also associated with specific features of animals' life cycles: the young are born relatively well-developed rather than helpless; and the death-rate among adults is high.

Respiratory System

Air sacs



Birds' lungs obtain fresh air during both exhalation and inhalation, because the air sacs do all the "pumping" and the lungs simply absorb oxygen.

From about 1870 onwards scientists have generally agreed that the post-cranial skeletons of many dinosaurs contained many air-filled cavities (postcranial skeletal pneumaticity, especially in the vertebrae. Pneumatization of the skull (such as paranasal sinuses) is found in both synapsids and archosaurs, but postcranial pneumatization is found only in birds, non-avian saurischian dinosaurs, and pterosaurs.

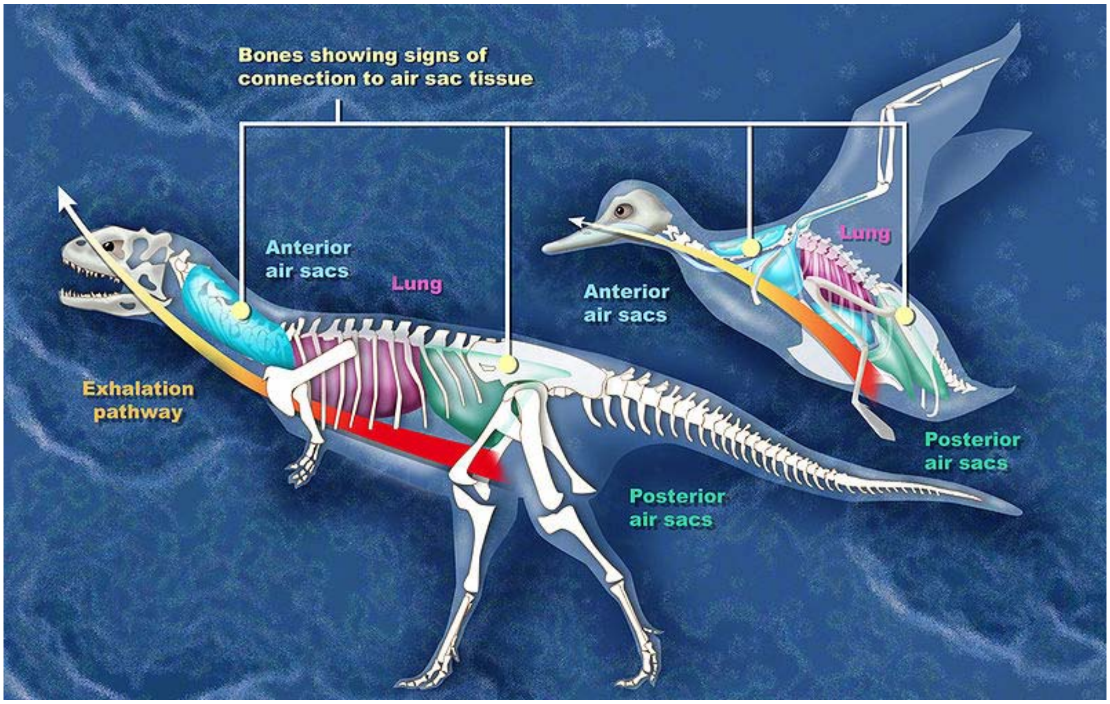
For a long time these cavities were regarded simply as weight-saving devices, but Bakker proposed that they contained air sacs like those which make birds' respiratory systems the most efficient of all animals'.

John Ruben *et al.* (1997, 1999, 2003, 2004) disputed this and suggested that dinosaurs had a "tidal" respiratory system (in and out) powered by a crocodile-like hepatic piston mechanism - muscles attached mainly to the pubis pull the liver backwards, which makes the lungs expand to inhale; when these muscles relax, the lungs return to their previous size and shape, and the animal exhales. They also presented this as a reason for doubting that birds descended from dinosaurs.

Critics have claimed that, without avian air sacs, modest improvements in a few aspects of a modern reptile's circulatory and respiratory systems would enable the reptile to achieve 50% to 70% of the oxygen flow of a mammal of similar size, and that lack of avian air sacs would not prevent the development of endothermy. Very few formal rebuttals have been published in scientific journals of Ruben *et al.*'s claim that dinosaurs could not have had avian-style air sacs; but one points out that the *Sinosauropteryx* fossil on which they based much of their argument was severely flattened and therefore it was impossible to tell whether the liver was the right shape to act as part of a hepatic piston mechanism. Some recent papers simply note without further comment that Ruben *et al.* argued against the presence of air sacs in dinosaurs.

Researchers have presented evidence and arguments for air sacs in sauropods, "prosauropods", coelurosaurs, ceratosaurs, and the theropods *Aerosteon* and *Coelophysis*.

In advanced sauropods ("neosauropods") the vertebrae of the lower back and hip regions show signs of air sacs. In early sauropods only the cervical (neck) vertebrae show these features. If the developmental sequence found in bird embryos is a guide, air sacs actually evolved before the channels in the skeleton that accommodate them in later forms.



Comparison between the air sacs of *Majungasaurus* and a bird

Evidence of air sacs has also been found in theropods. Studies indicate that fossils of coelurosaurs, ceratosaurs, and the theropods *Coelophysis* and *Aerosteon* exhibit evidence of air sacs. *Coelophysis*, from the late Triassic, is one of the earliest dinosaurs whose fossils show evidence of channels for air sacs. *Aerosteon*, a Late Cretaceous allosaur, had the most bird-like air sacs found so far.

Early sauropodomorphs, including the group traditionally called "prosauropods", may also have had air sacs. Although possible pneumatic indentations have been found in *Plateosaurus* and *Thecodontosaurus*, the indentations are very small. One study in 2007 concluded that prosauropods likely had abdominal and cervical air sacs, based on the evidence for them in sister taxa (theropods and sauropods). The study concluded that it was impossible to determine whether prosauropods had a bird-like flow-through lung, but that the air sacs were almost certainly present. A further indication for the presence of air sacs and their use in lung ventilation comes from a reconstruction of the air exchange volume (the volume of air exchanged with each breath) of *Plateosaurus*, which when expressed as a ratio of air volume per body weight at 29 ml/kg is similar to values of geese and other birds, and much higher than typical mammalian values.

So far no evidence of air sacs has been found in ornithischian dinosaurs. But this does not imply that ornithischians could not have had metabolic rates comparable to those of mammals, since mammals also do not have air sacs.

Three explanations have been suggested for the development of air sacs in dinosaurs:

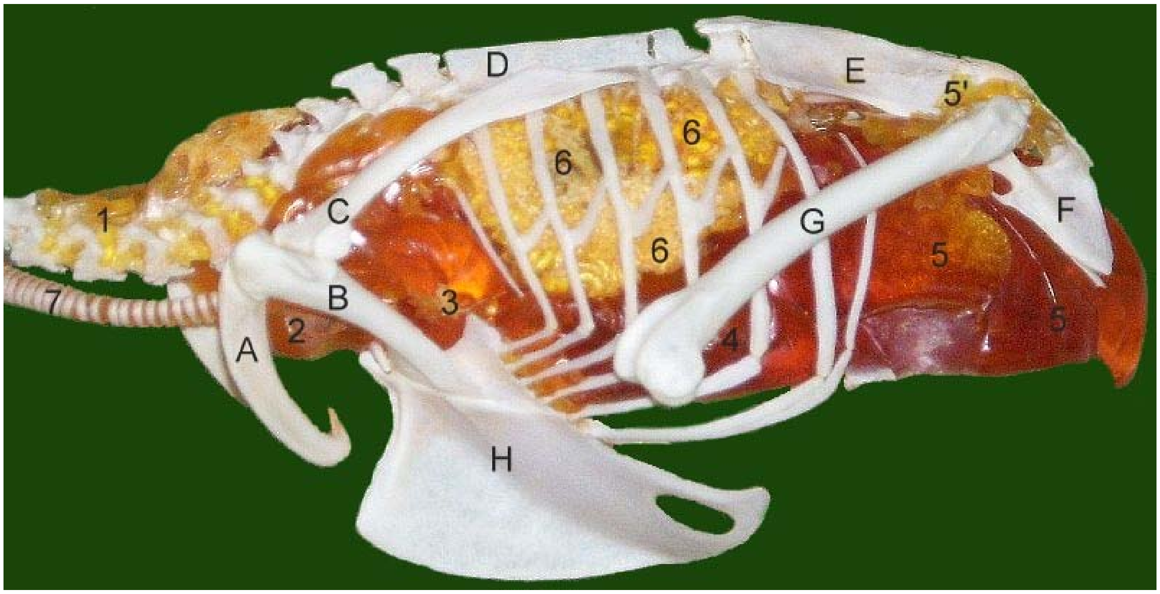
- Increase in respiratory capacity. This is probably the most common hypothesis, and fits well with the idea that many dinosaurs had fairly high metabolic rates.
- Improving balance and maneuvrability by lowering the center of gravity and reducing rotational inertia. However this does not explain the expansion of air sacs in the quadrupedal sauropods.
- As a cooling mechanism. It seems that air sacs and feathers evolved at about the same time in coelurosaurs. If feathers retained heat, their owners would have required a means of dissipating excess heat. This idea is plausible but needs further empirical support.

Calculations of the volumes of various parts of the sauropod *Apatosaurus*’ respiratory system support the evidence of bird-like air sacs in sauropods:

- Assuming that *Apatosaurus*, like dinosaurs' nearest surviving relatives crocodilians and birds, did not have a diaphragm, the dead-space volume of a 30-ton specimen would be about 184 liters. This is the total volume of the mouth, trachea and air tubes. If the animal exhales less than this, stale air is not expelled and is sucked back into the lungs on the following inhalation.
- Estimates of its tidal volume – the amount of air moved into or out of the lungs in a single breath – depend on the type of respiratory system the animal had: 904 liters if avian; 225 liters if mammalian; 19 liters if reptilian.

On this basis, *Apatosaurus* could not have had a reptilian respiratory system, as its tidal volume would have been less than its dead-space volume, so that stale air was not expelled but was sucked back into the lungs. Likewise, a mammalian system would only provide to the lungs about 225 − 184 = 41 liters of fresh, oxygenated air on each breath. *Apatosaurus* must therefore have had either a system unknown in the modern world or one like birds', with multiple air sacs and a flow-through lung. Furthermore, an avian system would only need a lung volume of about 600 liters while a mammalian one would have required about 2,950 liters, which would exceed the estimated 1,700 liters of space available in a 30-ton *Apatosaurus'* chest.

Dinosaur respiratory systems with bird-like air sacs may have been capable of sustaining higher activity levels than mammals of similar size and build can sustain. In addition to providing a very efficient supply of oxygen, the rapid airflow would have been an effective cooling mechanism, which is essential for animals that are active but too large to get rid of all the excess heat through their skins.



The uncinate processes are the small white spurs about half-way along the ribs. The rest of this diagram shows the air sacs and other parts of a bird's respiratory system:1 cervical air sac, 2 clavicular air sac, 3 cranial thoracal air sac, 4 caudal thoracal air sac, 5 abdominal air sac (5' diverticulus into pelvic girdle), 6 lung, 7 trachea

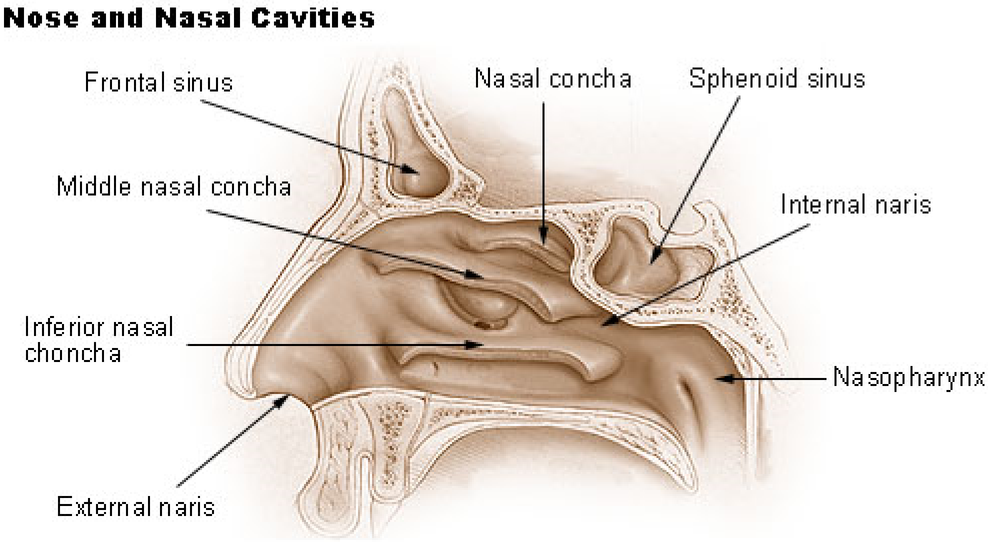
Uncinate processes on the ribs

Birds have spurs called "uncinate processes" on the rear edges of their ribs, and these give the chest muscles more leverage when pumping the chest to improve oxygen supply. The size of the uncinate processes is related to the bird's lifestyle and oxygen requirements: they are shortest in walking birds and longest in diving birds, which need to replenish their oxygen reserves quickly when they surface. Non-avian maniraptoran dinosaurs also had these uncinate processes and they were proportionately as long as in modern diving birds, a fact which indicates that maniraptorans needed a high-capacity oxygen supply.

Plates which may have functioned as in the same way as uncinate processes have been reported in fossils of the ornithischian dinosaur *Thescelosaurus*, and have been interpreted as evidence of high oxygen consumption and therefore high metabolic rate.

Nasal turbinates

Nasal turbinates (often referred to as "turbinals" or "conchae") are convoluted structures of thin bone in the nasal cavity. In most mammals and birds these are present and lined with mucous membranes which perform two functions: they improve the sense of smell by increasing the area available to absorb airborne chemicals; and they warm and moisten inhaled air and extract heat and moisture from exhaled air, to prevent desiccation of the lungs.



Human nasal turbinates/conchae are rather simple, but similar in position to those of other mammals.

Ruben *et al.* have argued in several papers that:

- No evidence of nasal turbinates has been found in dinosaurs (the papers focussed on coelurosaurs)
- All the dinosaurs they examined had nasal passages that were too narrow and short to accommodate nasal turbinates.
- Hence dinosaurs could not have sustained the breathing rate required for a mammal-like or bird-like metabolic rate while at rest, because their lungs would have dried out.

However, objections have been raised against this argument:

- Nasal turbinates are absent or very small in some birds (e.g. ratites, Procellariiformes and Falconiformes) and mammals (e.g. whales, anteaters, bats, elephants, and most primates), although these animals are fully endothermic and in some cases very active.
- Other studies conclude that nasal passages of these dinosaurs were long enough and wide enough to accommodate nasal turbinates or similar mechanisms to avoid desiccation of the lungs.
- Nasal turbinates are fragile and seldom found in fossils. In particular none have been found in fossil birds.

Cardiovascular system

The possible heart of "Willo" the thescelosaur (center).

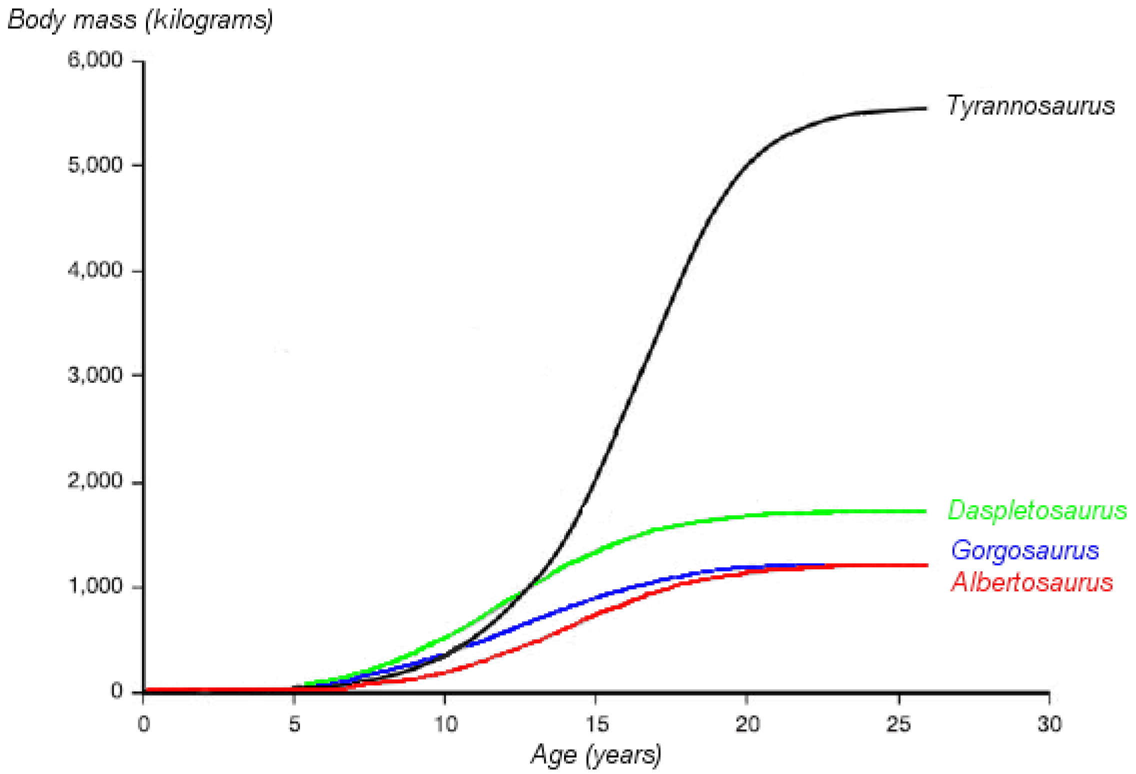
In principle one would expect dinosaurs to have had two-part circulations driven by four-chambered hearts, since many would have needed high blood pressure to deliver blood to their heads, which were high off the ground, but vertebrate lungs can only tolerate fairly low blood pressure. In 2000, a skeleton of *Thescelosaurus*, now on display at the North Carolina Museum of Natural Sciences, was described as including the remnants of a four-chambered heart and an aorta. The authors interpreted the structure of the heart as indicating an elevated metabolic rate for *Thescelosaurus*, not reptilian cold-bloodedness. Their conclusions have been disputed; other researchers published a paper where they assert that the heart is really a concretion of entirely mineral "cement". As they note: the anatomy given for the object is incorrect, for example the alleged "aorta" is narrowest where it meets the "heart" and lacks arteries branching from it; the "heart" partially engulfs one of the ribs and has an internal structure of concentric layers in some places; and another concretion is preserved behind the right leg. The original authors defended their position; they agreed that the chest did contain a type of concretion, but one that had formed around and partially preserved the more muscular portions of the heart and aorta.

Regardless of the object's identity, it may have little relevance to dinosaurs' internal anatomy and metabolic rate. Both modern crocodilians and birds, the closest living relatives of dinosaurs, have four-chambered hearts, although modified in crocodilians, and so dinosaurs probably had them as well. However such hearts are not necessarily tied to metabolic rate.

Growth and lifecycle

No dinosaur egg has been found that is larger than a basketball and embryos of large dinosaurs have been found in relatively small eggs, e.g. Maiasaura. Like mammals, dinosaurs stopped growing when they reached the typical adult size of their species, while mature reptiles continue to grow slowly if they have enough food. Dinosaurs of all sizes grew faster than similarly-sized modern reptiles; but the results of comparisons with similarly-sized "warm-blooded" modern animals depend on their sizes:

Weight (kg)	Comparative growth rate of dinosaurs	Modern animals in this size range
0.22	Slower than marsupials	Rat
1 - 20	Similar to marsupials, slower than precocial birds (those that are born capable of running)	From guinea pig to Andean Condor
100 - 1000	Faster than marsupials, similar to precocial birds, slower than placental mammals	From Red Kangaroo to Polar Bear
1500 – 3500	Similar to most placental mammals	From American Bison to rhinoceros
25000 and over	Very fast, similar to modern whales; but about half that of a scaled-up altricial bird (one that is born helpless) - if one could scale up a bird to 25,000 kilograms (25 LT; 28 ST)	Whales



A graph showing the hypothesized growth curves (body mass versus age) of four tyrannosaurids. *Tyrannosaurus rex* is drawn in black. Based on Erickson et al. 2004.

Tyrannosaurus rex showed a "teenage growth spurt":

- ½ ton at age 10
- very rapid growth to around 2 tons in the mid-teens (about ½ ton per year).
- negligible growth after the second decade.

A 2008 study of one skeleton of the hadrosaur *Hypacrosaurus* concluded that this dinosaur grew even faster, reaching its full size at the age of about 15; the main evidence was the number and spacing of growth rings in its bones. The authors found this consistent with a life-cycle theory that prey species should grow faster than their predators if they lose a lot of juveniles to predators and the local environment provides enough resources for rapid growth.

It appears that individual dinosaurs were rather short-lived, e.g. the oldest (at death) *Tyrannosaurus* found so far was 28 and the oldest sauropod was 38. Predation was probably responsible for the high death rate of very young dinosaurs and sexual competition for the high death rate of sexually mature dinosaurs.

Metabolism

Scientific opinion about the life-style, metabolism and temperature regulation of dinosaurs has varied over time since the discovery of dinosaurs in the mid-19th century. Scientists have broadly disagreed as to whether dinosaurs were capable of regulating their body temperatures at all. More recently, the **warm-bloodedness of dinosaurs** (more specifically, active lifestyle and at least fairly constant temperature) has become the consensus view, and debate has focused on the mechanisms of temperature regulation and how similar dinosaurs' metabolic rate was to that of birds and mammals.

What the debate is about

"Warm-bloodedness" is a complex and rather ambiguous term, because it includes some or all of:

- **Homeothermy**, i.e. maintaining a fairly constant body temperature. Modern endotherms maintain a variety of temperatures: 28 °C (82 °F) to 30 °C (86 °F) in monotremes and sloths; 33 °C (91 °F) to 36 °C (97 °F) in marsupials; 36 °C (97 °F) to 38 °C (100 °F) in most placentals; and around 41 °C (106 °F) in birds.
- **Tachymetabolism**, i.e. maintaining a high metabolic rate, particularly when at rest. This requires a fairly high and stable body temperature, since: biochemical processes run about half as fast if an animal's temperature drops by 10C°; most enzymes have an optimum operating temperature and their efficiency drops rapidly outside the preferred range.
- **Endothermy**, i.e. the ability to generate heat internally, for example by "burning" fat, rather than via behaviors such as basking or muscular activity. Although endothermy is in principle the most reliable way to maintain a fairly constant temperature, it is expensive, for example modern mammals need 10 to 13 times as much food as modern reptiles.

Large dinosaurs may also have maintained their temperatures by inertial homeothermy, also known as "bulk homeothermy" or "mass homeothermy". In other words, the thermal capacity of such large animals was so high that that it would take two days or more for their temperatures to change significantly, and this would have smoothed out variations caused by daily temperature cycles. This smoothing effect has been observed in large turtles and crocodilians, but *Plateosaurus*, which weighed about 700 kilograms (1,500 lb), may have been the smallest dinosaur in which it would have been effective. Inertial homeothermy would not have been possible for small species nor for the young of larger species. Vegetation fermenting in the guts of large herbivores can also produce considerable heat, but this method of maintaining a high and stable temperature would not have been possible for carnivores nor for small herbivores or the young of larger herbivores.

Since the internal mechanisms of extinct creatures are unknowable, most discussion focuses on homeothermy and tachymetabolism.

Assessment of metabolic rates is complicated by the distinction between the rates while resting and while active. In all modern reptiles and most mammals and birds the maximum rates during all-out activity are 10 to 20 times higher than minimum rates while at rest. However in a few mammals these rates differ by a factor of 70. Theoretically it would be possible for a land vertebrate to have a reptilian metabolic rate at rest and a bird-like rate while working flat out. However an animal with such a low resting rate would be unable to grow quickly. The huge herbivorous sauropods may have been on the move so constantly in search of food that their energy expenditure would have been much the same irrespective of whether their resting metabolic rates were high or low.

Metabolic options

The main possibilities are that:

- Dinosaurs were cold-blooded, like modern reptiles, except that the large size of many would have stabilized their body temperatures.
- They were warm-blooded, more like modern mammals or birds than modern reptiles.
- They were neither cold-blooded nor warm-blooded in modern terms, but had metabolisms that were different from and some ways intermediate between those of modern cold-blooded and warm-blooded animals.
- They included animals with two or three of these types of metabolism.

Dinosaurs were around for about 150 million years, so it is very likely that different groups evolved different metabolisms and thermoregulatory regimes, and that some developed different physiologies from the first dinosaurs.

If all or some dinosaurs had intermediate metabolisms, they may have had the following features:

- Low resting metabolic rates, which would reduce the amount of food needed to keep them ticking over and allow more of it to be used for growth than in animals with high resting metabolic rates.
- Inertial homeothermy
- The ability to control heat loss by expanding and contracting blood vessels just under the skin, as many modern reptiles do.
- Two-part circulations driven by four-chambered hearts.
- High aerobic capacity, allowing sustained activity.

Robert Reid has suggested that such animals could be regarded as "failed endotherms". He envisaged both dinosaurs and the Triassic ancestors of mammals passing through a stage with these features. Mammals were forced to become smaller as archosaurs came to dominate ecological niches for medium to large animals. Their decreasing size made them more vulnerable to heat loss because it increased their ratios of surface area to mass, and thus forced them to increase internal heat generation and thus become full endotherms. On the other hand dinosaurs became medium to very large animals and thus were able to retain the "intermediate" type of metabolism.

Bone structure

Armand de Ricqlès discovered Haversian canals in dinosaur bones, and argued that they were evidence of endothermy in dinosaurs. These canals are common in "warm-blooded" animals and are associated with fast growth and an active life style because they help to recycle bone in order to facilitate rapid growth and to repair damage caused by stress or injuries. Bakker argued that the presence of fibrolamellar bone (produced quickly and having a fibrous, woven appearance) in dinosaur fossils was evidence of endothermy.

However as a result of other, mainly later research, bone structure is not considered a reliable indicator of metabolism in dinosaurs, mammals or reptiles:

- Dinosaur bones often contain growth rings, formed by alternating periods of slow and fast growth; in fact many studies count growth rings to estimate the ages of dinosaurs. The formation of growth rings is usually driven by seasonal changes in temperature, and this seasonal influence has sometimes been regarded as a sign of slow metabolism and ectothermy. But growth rings are found in polar bears and in mammals that hibernate.
- Fibrolamellar bone is fairly common in young crocodilians and sometimes found in adults.
- Haversian bone has been found in turtles, crocodilians and tortoises, but is often absent in small birds, bats, shrews and rodents.

Nevertheless de Ricqlès persevered with studies of the bone structure of dinosaurs and archosaurs. In mid-2008 he co-authored a paper which examined bone samples from a wide range of archosaurs, including early dinosaurs, and which concluded that:

- Even the earliest archosauriformes may have been capable of very fast growth, which suggests they had fairly high metabolic rates. Although drawing conclusions about the earliest archosauriformes from later forms is tricky, because species-specific variations in bone structure and growth rate are very likely, there are research strategies than can minimize the risk that such factors will cause errors in the analysis.
- Archosaurs split into three main groups in the Triassic: ornithodirans, from which dinosaurs evolved, remained committed to rapid growth; crocodilians' ancestors adopted more typical "reptilian" slow growth rates; and most other Triassic archosaurs had intermediate growth rates.

Growth rates

Dinosaurs grew from small eggs to several tons in weight relatively quickly. A natural interpretation of this is that that dinosaurs converted food into body weight very quickly, which requires a fairly fast metabolism both to forage actively and to assimilate the food quickly.

But a preliminary study of the relationship between adult size, growth rate, and body temperature concluded that larger dinosaurs had higher body temperatures than smaller ones had; *Apatosaurus*, the largest dinosaur in the sample, was estimated to have a body temperature exceeding 41 °C (106 °F), whereas smaller dinosaurs were estimated to have body temperatures around 25 °C (77 °F) – for comparison, normal human body temperature is about 37 °C (99 °F). Based on these estimations, the study concluded that large dinosaurs were inertial homeotherms (their temperatures were stabilized by their sheer bulk) and that dinosaurs were ectothermic (in colloquial terms, "cold-blooded", because they did not generate as much heat as mammals when not moving or digesting food). These results are consistent with the relationship between dinosaurs' sizes and growth rates (described above).

Oxygen isotope ratios in bone

The ratio of the isotopes ^{16}O and ^{18}O in bone depends on the temperature at which the bone was formed - the higher the temperature, the more ^{16}O. Barrick and Showers (1999) analyzed the isotope ratios in two theropods that lived in temperate regions with seasonal variation in temperature, *Tyrannosaurus* (USA) and *Giganotosaurus* (Argentina):

- dorsal vertebrae from both dinosaurs showed no sign of seasonal variation, indicating that both maintained a constant core temperature despite seasonal variations in air temperature.
- ribs and leg bones from both dinosaurs showed greater variability in temperature and a lower average temperature as the distance from the vertebrae increased.

Barrick and Showers concluded that both dinosaurs were endothermic but at lower metabolic levels than modern mammals, and that inertial homeothermy was an important part of their temperature regulation as adults. Their similar analysis of some Late Cretaceous ornithischians in 1996 concluded that these animals showed a similar pattern.

However this view has been challenged. The evidence indicates homeothermy, but by itself cannot prove endothermy. Secondly, the production of bone may not have been continuous in areas near the extremities of limbs – in allosaur skeketons lines of arrested growth ("LAGs"; rather like growth rings) are sparse or absent in large limb bones but common in the fingers and toes. While there is no absolute proof that LAGs are temperature-related, they could mark times when the extremities were so cool that the bones ceased to grow. If so, the data about oxygen isotope ratios would be incomplete, especially for times when the extremities were coolest. Oxygen isotope ratios may be an unreliable method of estimating temperatures if it cannot be shown that bone growth was equally continuous in all parts of the animal.

Predator-prey ratios

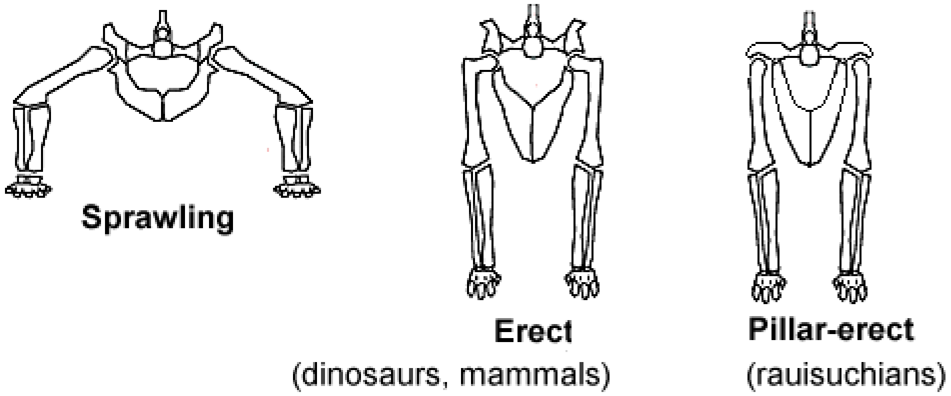
Bakker argued that:

- cold-blooded predators need much less food than warm-blooded ones, so a given mass of prey can support far more cold-blooded predators than warm-blooded ones.
- the ratio of the total mass of predators to prey in dinosaur communities was much more like that of modern and recent warm-blooded communities than that of recent or fossil cold-blooded communities.
- hence predatory dinosaurs were warm-blooded. And since the earliest dinosaurs (e.g. *Staurikosaurus*, *Herrerasaurus*) were predators, all dinosaurs must have been warm-blooded.

This argument was criticized on several grounds and is no longer taken seriously (the following list of criticisms is far from exhaustive):

- Estimates of dinosaur weights vary widely, and even a small variation can make a large difference to the calculated predator-prey ratio.
- His sample may not have been representative. Bakker obtained his numbers by counting museum specimens, but these have a bias towards rare or especially well-preserved specimens, and do not represent what exists in fossil beds. Even fossil beds may not accurately represent the actual populations, for example smaller and younger animals have less robust bones and are therefore less likely to be preserved.
- There are no published predator-prey ratios for large ectothermic predators, because such predators are very rare and mostly occur only on fairly small islands. Large ectothermic herbivores are equally rare. So Bakker was forced to compare mammalian predator-prey ratios with those of fish and invertebrate communities, where life expectancies are much shorter and other differences also distort the comparison.
- The concept assumes that predator populations are limited only by the availability of prey. However other factors such as shortage of nesting sites, cannibalism or predation of one predator on another can hold predator populations below the limit imposed by prey biomass, and this would misleadingly reduce the predator-prey ratio. .
- Ecological factors can misleadingly reduce the predator-prey ratio, for example: a predator might prey on only some of the "prey" species present; disease, parasites and starvation might kill some of the prey animals before the predators get a chance to hunt them.
- It is very difficult to state precisely what preys on what. For example the young of herbivores may preyed upon by lizards and snakes while the adults are preyed on by mammals. Conversely the young of many predators live largely on invertrebrates and switch to vertrebrate as they grow.

Posture and gait



Hip joints and limb postures.

Dinosaurs' limbs were erect and held under their bodies, rather than sprawling out to the sides like those of lizards and newts. The evidence for this is the angles of the joint surfaces and the locations of muscle and tendon attachments on the bones. Attempts to represent dinosaurs with sprawling limbs result in creatures with dislocated hips, knees, shoulders and elbows.

Carrier's constraint states that air-breathing vertebrates which have 2 lungs and flex their bodies sideways during locomotion find it very difficult to move and breathe at the same time. This severely limits their stamina and forces them to spend more time resting than moving.

Sprawling limbs require sideways flexing during locomotion (except for tortoises and turtles, which are very slow and whose armor keeps their bodies fairly rigid). But despite Carrier's constraint sprawling limbs are efficient for creatures which spend most of their time resting on their bellies and only move for a few seconds at a time, because this arrangement minimizes the energy costs of getting up and lying down.

Erect limbs increase the costs of getting up and lying down, but avoid Carrier's constraint. This indicates that dinosaurs were active animals because natural selection would have favored the retention of sprawling limbs if dinosaurs had been sluggish and spent most of their waking time resting. An active lifestyle requires a metabolism which quickly regenerates energy supplies and breaks down waste products which cause fatigue, i.e. it requires a fairly fast metabolism and a considerable degree of homeothermy.

Bakker and Ostrom both pointed out that all dinosaurs had erect hindlimbs and that all quadrupedal dinosaurs except the ceratopsians and ankylosaurs had erect forelimbs; and that among living animals only the endothermic ("warm-blooded") mammals and birds have erect limbs (Ostrom acknowledged that crocodilians' occasional "high walk" was a partial exception). Bakker claimed this was clear evidence of endothermy in dinosaurs, while Ostrom regarded it as persuasive but not conclusive.

A 2009 study supported the hypothesis that endothermy was widespread in at least larger non-avian dinosaurs, and that It was plausibly ancestral for all dinosauriforms, based on the biomechanics of running.

Feathers

Skin impression of the hadrosaur *Edmontosaurus*

There is now no doubt that many theropod dinosaur species had feathers, including *Shuvuuia*, *Sinosauropteryx* and *Dilong* (an early tyrannosaur). These have been interpreted as insulation and therefore evidence of warm-bloodedness.

But impressions of feathers have only been found in coelurosaurs (which includes the ancestors of both birds and tyrannosaurs), so at present feathers give us no information about the metabolisms of the other major dinosaur groups, e.g. coelophysids, ceratosaurs, carnosaurs, sauropods or ornithischians.

In fact the fossilised skin of *Carnotaurus* (an abelisaurid and therefore not a coelurosaur) shows an unfeathered, reptile-like skin with rows of bumps. But an adult *Carnotaurus* weighed about 1 ton, and mammals of this size and larger have either very short hair or naked skins, so perhaps the skin of *Carnotaurus* tells us nothing about whether smaller non-coelurosaurid theropods had feathers.

Skin-impressions of *Pelorosaurus* and other sauropods (dinosaurs with elephantine bodies and long necks) reveal large hexagonal scales, and some sauropods, such as *Saltasaurus*, had bony plates in their skin. The skin of ceratopsians consisted of large polygonal scales, sometimes with scattered circular plates. "Mummified" remains and skin impressions of hadrosaurids reveal pebbly scales. It is unlikely that the ankylosaurids, such as *Euoplocephalus*, had insulation, as most of their surface area was covered in bony knobs and plates. Likewise there is no evidence of insulation in the stegosaurs.

Polar dinosaurs

Dinosaur fossils have been found in regions that were close to the poles at the relevant times, notably in southeastern Australia, Antarctica and the North Slope of Alaska. There is no evidence of major changes in the angle of the Earth's axis, so polar dinosaurs and the rest of these ecosystems would have had to cope with the same extreme variation of day length through the year that occurs at similar latitudes today (up to a full day with no darkness in summer, and a full day with no sunlight in winter).

Studies of fossilized vegetation suggest that the Alaska North Slope had a maximum temperature of 13 °C (55 °F) and a minimum temperature of 2 °C (36 °F) to 8 °C (46 °F) in the last 35 million years of the Cretaceous (slightly cooler than Portland, Oregon but slightly warmer than Calgary, Alberta). Even so, the Alaska North Slope has no fossils of large cold-blooded animals such as lizards and crocodilians, which were common at the same time in Alberta, Montana, and Wyoming. This suggests that at least some non-avian dinosaurs were warm-blooded. It has been proposed that North American polar dinosaurs may have migrated to warmer regions as winter approached, which would allow them to inhabit Alaska during the summers even if they were cold-blooded. But a round trip between there and Montana would probably have used more energy than a cold-blooded land vertebrate produces in a year; in other words the Alaskan dinosaurs would have had to be warm-blooded irrespective of whether they migrated or stayed for the winter. A 2008 paper on dinosaur migration by Phil R. Bell and Eric Snively proposed that most polar dinosaurs, including theropods, sauropods, ankylosaurians, and hypsilophodonts, probably overwintered, although hadrosaurids like *Edmontosaurus* were probably capable of annual 2,600 km (1,600 mile) round trips.

It is more difficult to determine the climate of southeastern Australia when the dinosaur fossil beds were laid down 115 to 105 million years ago, towards the end of the Early Cretaceous: these deposits contain evidence of permafrost, ice wedges, and hummocky ground formed by the movement of subterranean ice, which suggests mean annual temperatures ranged between −6 °C (21.2 °F) and 5 °C (41 °F); oxygen isotope studies of these deposits give a mean annual temperature of 1.5 °C (34.7 °F) to 2.5 °C (36.5 °F). However the diversity of fossil vegetation and the large size of some of fossil trees exceed what is found in such cold environments today, and no-one has explained how such vegetation could have survived in the cold temperatures suggested by the physical indicators – for comparison Fairbanks, Alaska presently has a mean annual temperature of 2.9 °C (37.2 °F). An annual migration from and to southeastern Australia would have been very difficult for fairly small dinosaurs in such as *Leaellynasaura*, a vegetarian about 60 centimetres (2.0 ft) to 90 centimetres (3.0 ft) long, because seaways to the north blocked the passage to warmer latitudes. Bone samples from *Leaellynasaura* and *Timimus*, an ornithomimid about 3.5 metres (11 ft) long and 1.5 metres (4.9 ft) high at the hip, suggested these two dinosaurs had different ways of surviving the cold, dark winters: the *Timimus* sample had lines of arrested growth (LAGs for short; similar to growth rings), and it may have hibernated; but the *Leaellynasaura* sample showed no signs of LAGs, so it may have remained active throughout the winter.

Evidence for behavioral thermoregulation

Some dinosaurs, e.g. *Spinosaurus* and *Ouranosaurus*, had on their backs "sails" supported by spines growing up from the vertebrae. (This was also true, incidentally, for the synapsid *Dimetrodon*.) Such dinosaurs could have used these sails to:

- take in heat by basking with the "sails" at right angles to the sun's rays.
- to lose heat by using the "sails" as radiators while standing in the shade or while facing directly towards or away from the sun.

But these were a very small minority of all the dinosaur species which are known. One common interpretation of the plates on stegosaurs' backs is as heat exchangers for thermoregulation, as the plates are filled with blood vessels which could theoretically absorb and dissipate heat.
This might have worked for a stegosaur with large plates, such as *Stegosaurus*, but other stegosaurs, such as *Wuerhosaurus*, *Tuojiangosaurus* and *Kentrosaurus* possessed much smaller plates with a surface area of doubtful value for thermo-regulation. However, the idea of stegosaurian plates as heat exchangers has recently been questioned.

The crocodilian puzzle and early archosaur metabolism

It appears that the earliest dinosaurs had the features on which the arguments for warm-blooded dinosaurs are based - especially erect limbs. This raises the question "How did dinosaurs become warm-blooded?" The most obvious possible answers are:

- "Their immediate ancestors (archosaurs) were cold-blooded, and dinosaurs began developing warm-bloodedness very early in their evolution." This would imply that dinosaurs developed a significant degree of warm-bloodedness in a very short time, possibly less than 20M years. But in mammals' ancestors the evolution of warm-bloodedness seems to have taken much longer, starting with the beginnings of a secondary palate around the beginning of the mid-Permian and going on possibly until the appearance of hair about 164M years ago in the mid Jurassic).
- "Dinosaurs' immediate ancestors (archosaurs) were at least fairly warm-blooded, and dinosaurs evolved further in that direction." This answer raises 2 problems: (**A**) The early evolution of archosaurs is still very poorly understood - large numbers of individuals and species are found from the start of the Triassic but only 2 species are known from the very late Permian (*Archosaurus rossicus* and *Protorosaurus speneri*); (**B**) Crocodilians evolved shortly before dinosaurs and are closely related to them, but are cold-blooded.

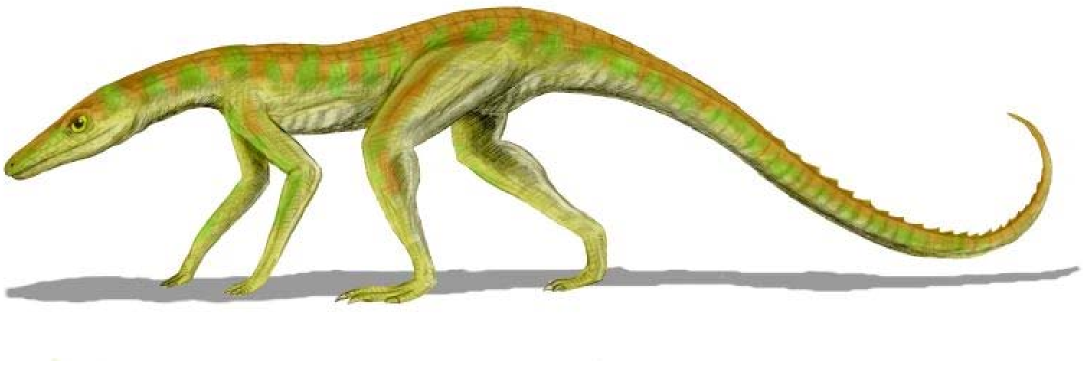
Crocodilians present some puzzles if one regards dinosaurs as active animals with fairly constant body temperatures. Crocodilians evolved shortly before dinosaurs and, second to birds, are dinosaurs' closest living relatives - but modern crocodilians are cold-blooded. This raises some questions:

- If dinosaurs were to a large extent "warm-blooded", when and how fast did warm-bloodedness evolve in their lineage?
- Modern crocodilians are cold-blooded but have several features associated with warm-bloodedness. How did they acquire these features?

Modern crocodilians are cold-blooded, but they can move with their limbs erect and they have several features which are normally associated with warm-bloodedness because they improve the animal's oxygen supply:

- 4-chambered hearts. Mammals and birds have 4-chambered hearts. Non-crocodilian reptiles have 3-chambered hearts, which are less efficient because they allow oxygenated and de-oxygenated blood to mix and therefore send some de-oxygenated blood out to the body instead of to the lungs. Modern crocodilians' hearts are 4-chambered, but are smaller relative to body size and run at lower pressure than those of modern mammals and birds. They also have a bypass which makes then functionally 3-chambered when under water, conserving oxygen.
- a diaphragm, which aids breathing.
- a secondary palate, which allows the animal to eat and breathe at the same time.
- a hepatic piston mechanism for pumping the lungs. This is different from the lung-pumping mechanisms of mammals and birds but similar to what some researchers claim to have found in some dinosaurs.

So why did natural selection favor the development of these features, which are very important for active warm-blooded creatures but of little apparent use to cold-blooded aquatic ambush predators which spend the vast majority of their time floating in water or lying on river banks?



Reconstruction of *Terrestrisuchus*, a very slim, leggy Triassic crocodylomorph.

It was suggested in the late 1980s that that crocodilians were originally active, warm-blooded predators and that their archosaur ancestors were warm-blooded. More recently, developmental studies have indicated that crocodilian embryos develop fully 4-chambered hearts first and then develop the modifications which make their hearts function as 3-chambered under water. Using the principle that ontogeny recapitulates phylogeny, the researchers concluded that the original crocodilians had fully 4-chambered hearts and were therefore warm-blooded and that later crocodilians developed the bypass as they reverted to being cold-blooded aquatic ambush predators.

More recent research on archosaur bone structures and their implications for growth rates also suggests that early archosaurs had fairly high metabolic rates and that the Triassic ancestors of crocodilians dropped back to more typically "reptilian" metabolic rates.

If this view is correct, the development of warm-bloodedness in archosaurs (reaching its peak in dinosaurs) and in mammals would have taken more similar amounts of time. It would also be consistent with the fossil evidence:

- The earliest crocodilians, e.g. *Terrestrisuchus*, were slim, leggy terrestrial predators.
- Erect limbs appeared quite early in archosaurs' evolution, and those of rauisuchians are very poorly adapted for any other posture.