An Introduction to Paleozoology

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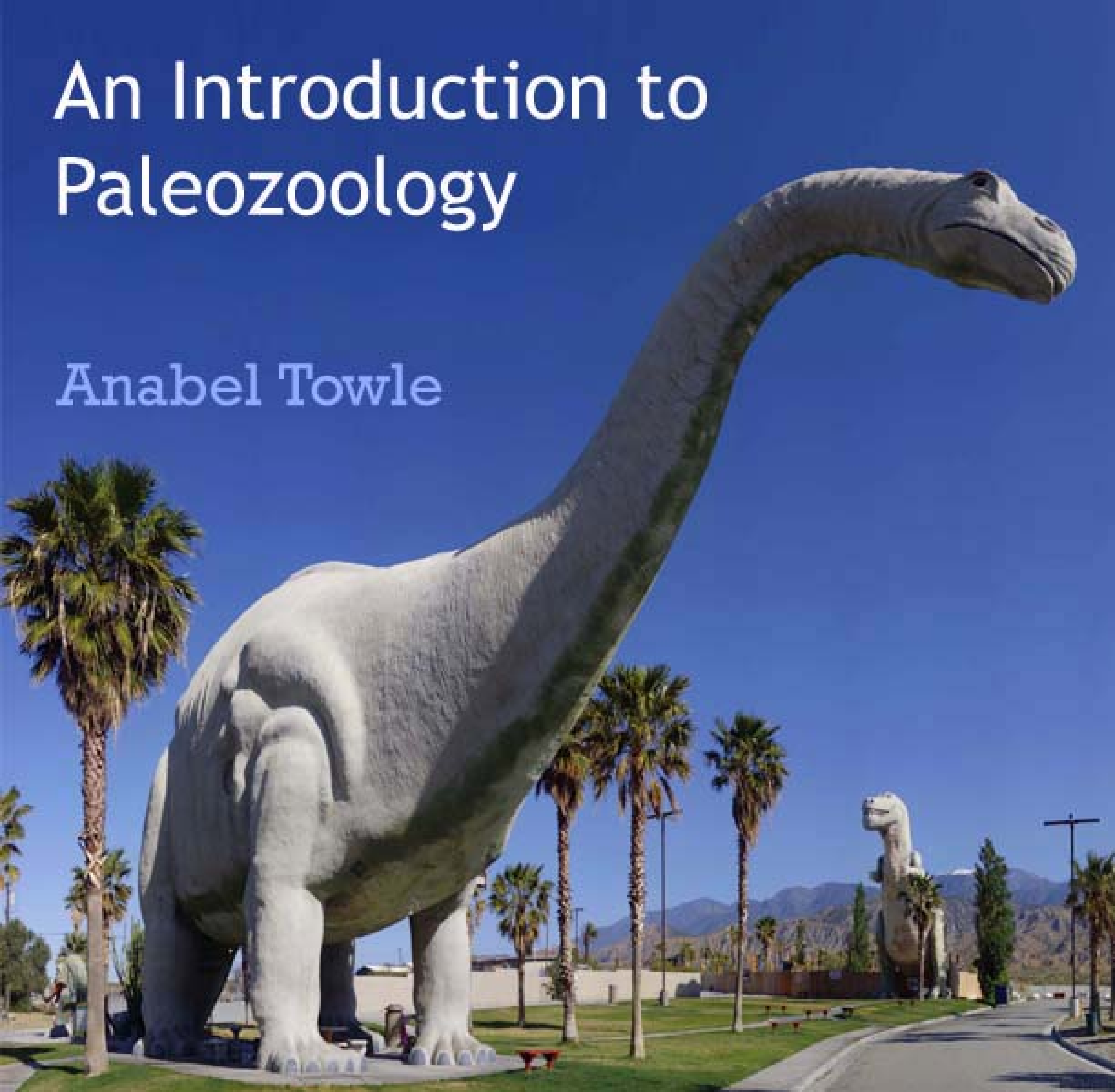

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Introduction

Paleozoology, also spelled as **palaeozoology**, is the branch of paleontology or paleobiology dealing with the recovery and identification of multicellular animal remains from geological (or even archeological) contexts, and the use of these fossils in the reconstruction of prehistoric environments and ancient ecosystems.

Definitive, macroscopic remains of these metazoans are found in the fossil record from the Ediacaran period of the Neoproterozoic era onwards, although they do not become common until the Late Devonian period in the latter half of the Paleozoic era.

Perhaps the best known macrofossils group is the dinosaurs. Other popularly known animal-derived macrofossils include trilobites, crustaceans, echinoderms, brachiopods, mollusks, bony fishes, sharks, Vertebrate teeth, and shells of numerous invertebrate groups. This is because hard organic parts, such as bones, teeth, and shells resist decay, and are the most commonly preserved and found animal fossils. Exclusively soft-bodied animals -- such as jellyfish, flatworms, nematodes, and insects -- are consequently rarely fossilized, as these groups do not produce hard organic parts.

Chapter 1

Dakota (Fossil) and Middle Miocene Disruption

Dakota (fossil)

Dakota is the nickname given to a fossil *Edmontosaurus* from the Hell Creek Formation in North Dakota. It is about 67 million years old, placing it in the Maastrichtian, the last stage of the Cretaceous period. It was about 11 m (35 ft) long and weighed about 3.5 tons.

The fossil is unusual and scientifically valuable because soft tissue including skin and muscle have been fossilized, giving researchers the rare opportunity to study more than bones, as with most vertebrate fossils. Preliminary research results indicate that hadrosaurs had heavier tails and were able to run faster than was previously thought.

Preservation

Dakota skin impression

Dinosaur fossils with Dakota's degree of preservation are extremely rare because many different factors must come together to allow it to occur. The carcass first must escape scavengers as well as degradation by the elements. The soft tissue must then be mineralized before it decomposes. Finally, as with all fossils, the mineralized body must escape destruction by geological forces over millions of years.

News reports have referred to Dakota as "mummified"; however, it is actually a fossil of a mummified dinosaur, where the animal's dried tissues have been transformed to rock through fossilization.

Discovery and analysis

Segment of the Dakota fossil

Dakota was first discovered by paleontology student Tyler Lyson on his family's North Dakota property in 1999 while he was a high school student, but he did not investigate the site in detail until 2004, when he discovered the soft tissue preservation. Lyson teamed with British paleontologist Phillip Manning, and the site was excavated in summer 2006.

Manning's team used a large-scale CT scanner, provided by NASA and the Boeing Company, to generate high-resolution scans of the preserved muscles and tendons of the rear legs. Because the intervertebral discs which space out the spinal column of the tail have been fossilized, researchers have been able to calculate its length more accurately. The preservation of its muscles and tendons allow the calculation of its mass. The results indicate the dinosaur could likely have run at 45 km/h (28 mph), faster than the estimated top speed of *Tyrannosaurus rex*, at 32 km/h (20 mph).

The well-preserved integument has retained its texture, and researchers have mapped it in three dimensions. The scales are of different sizes, and researchers speculate that their pattern may reflect the animal's coloration in life. For example, areas of an arm's joints are textured in what resembles a striped pattern.

Middle Miocene disruption

The term **Middle Miocene disruption,** alternatively the **Middle Miocene extinction** or **Middle Miocene extinction peak,** refers to a wave of extinctions of terrestrial and aquatic life forms that occurred around the middle of the Miocene Epoch, c. 14.8 to 14.5 million years ago, during the Langhian stage of the Miocene.

Madelaine Bohme observed the occurrence of Varanidae, Chamaeleon, Cordylidae, Tomistomidae, Alligatoridae, and giant turtles which indicate survival through the Miocene Climatic Optimum (18 to 16 Ma) in Central Europe (42W 45 N palaeolatitude). A major and permanent cooling step occurred between 14.8 and 14.1 Ma, associated with increased production of cold Antarctic deep waters and a major growth of the East Antarctic ice sheet. Two crocodiles of the genera *Gavialosuchus* and *Diplocynodon* were noted to have been extant in these northern latitudes prior to the permanent cooling step then became extinct 13.5 to 14 Ma.

A Middle Miocene delta ^{18}O increase, that is a relative increase in the heavier isotope of oxygen, has been noted in the Pacific, the Southern Ocean and the South Atlantic.

Chapter 2

Dinosaur

Dinosaurs
Temporal 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 [e]

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. The term is derived from the Greek words δεινός (*deinos* meaning "terrible", "powerful", or "wondrous") and σαῦρος (*sauros* meaning "lizard" or "reptile"). 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. For clarity, here we will use "dinosaur" as a synonym for "non-avian dinosaur". The term "non-avian dinosaur" will be used for emphasis as needed.

General description

Stegosaurus skeleton, Field Museum, Chicago

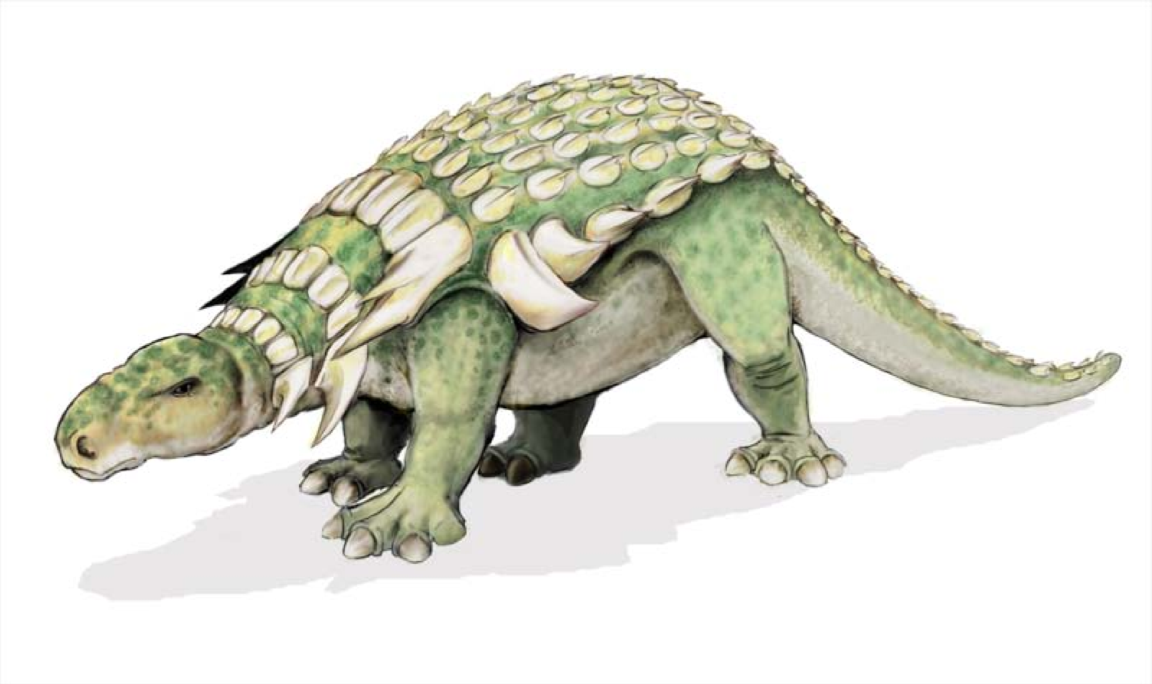
Using one of the above definitions, dinosaurs (aside from birds) can be generally described as terrestrial archosaurian reptiles with limbs held erect beneath the body, that existed from the Late Triassic (first appearing in the Carnian faunal stage) to the Late Cretaceous (going extinct at the end of 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

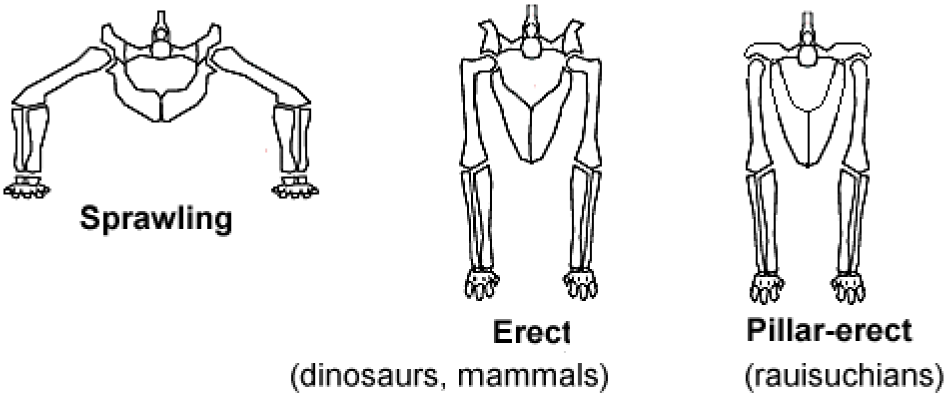
While recent discoveries have made it more difficult to present a universally agreed-upon list of dinosaurs' distinguishing features, nearly all dinosaurs discovered so far share certain modifications to the ancestral archosaurian skeleton. Although some later groups of dinosaurs featured further modified 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.

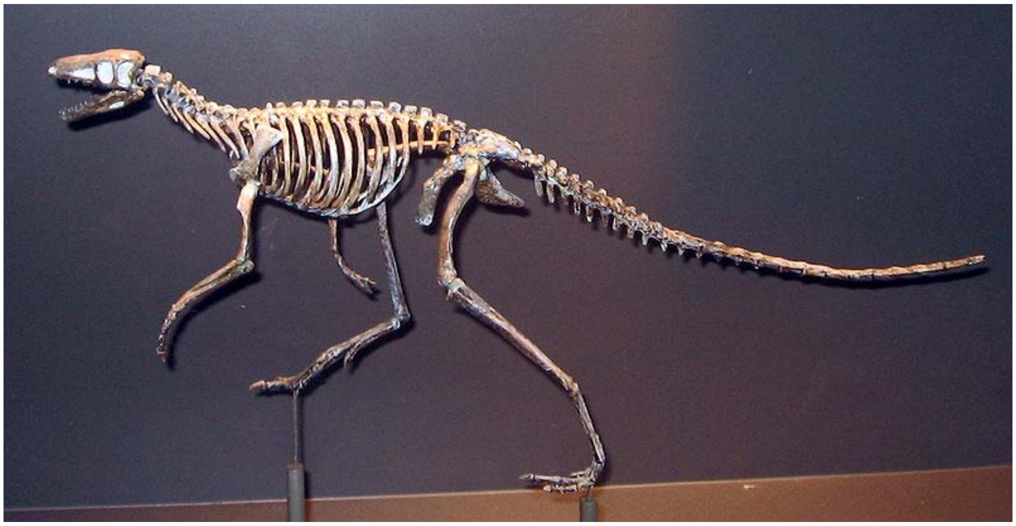


Hip joints and hindlimb postures

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

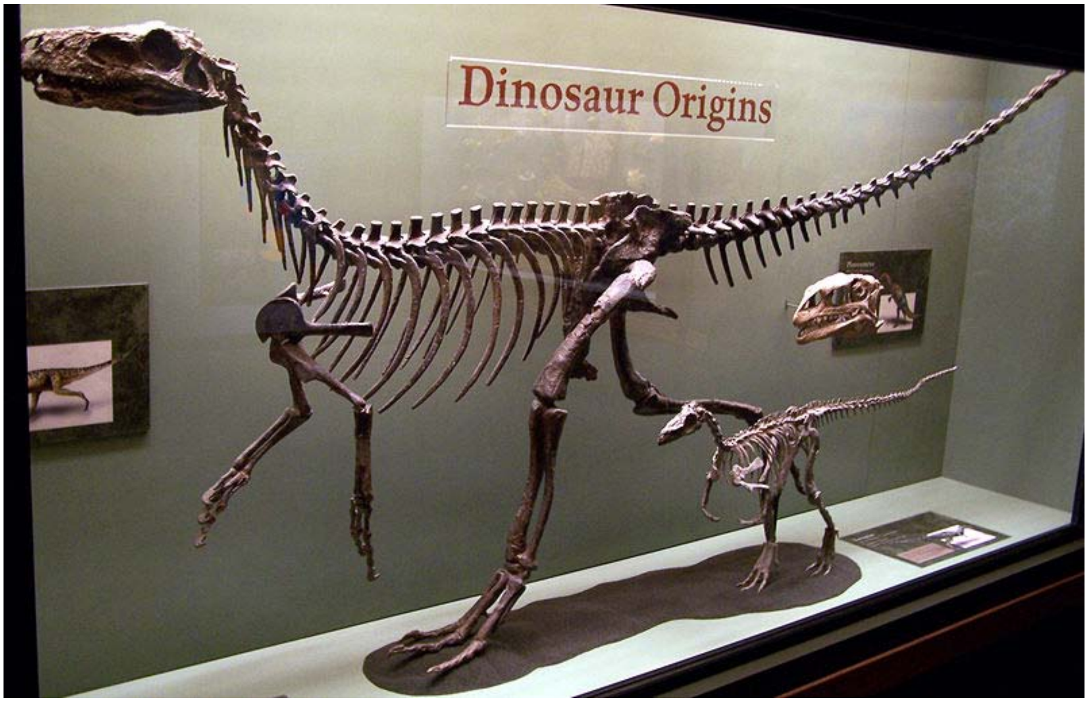


Marasuchus, a dinosaur-like ornithodiran

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

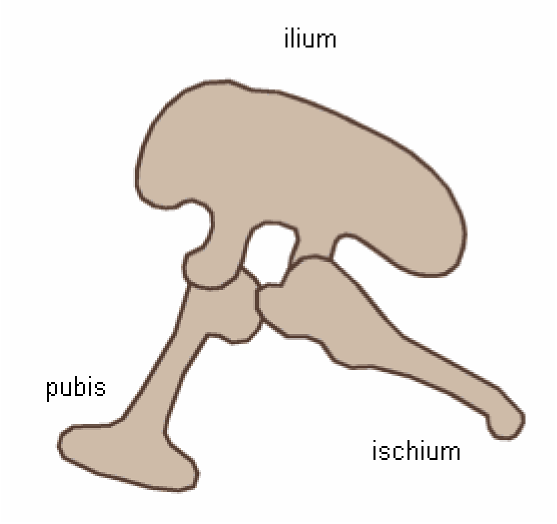
Statistical analyses based on raw data suggest that dinosaurs diversified, i.e. the number of species increased, in the Late Cretaceous. However in July 2008 Graeme T. Lloyd *et al.* argued that this apparent diversification was an illusion caused by sampling bias, because Late Cretaceous rocks have 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.

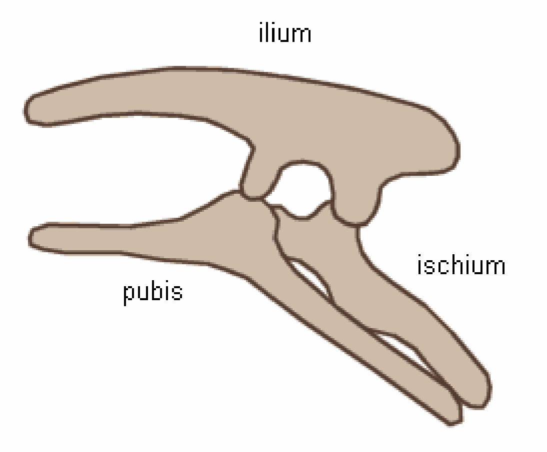
Collectively, dinosaurs are usually regarded as a superorder or an unranked clade. They are divided into two orders, Saurischia and Ornithischia, depending upon pelvic structure. Saurischia includes those taxa sharing a more recent common ancestor with birds than with Ornithischia, while Ornithischia 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)

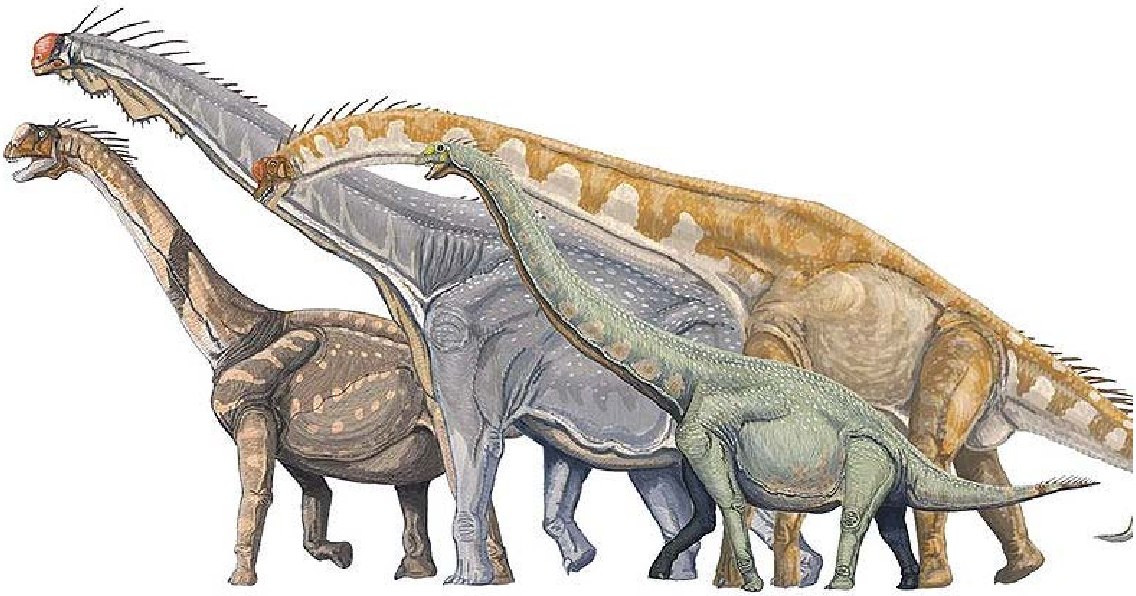
Tyrannosaurus pelvis (showing saurischian structure – left side)



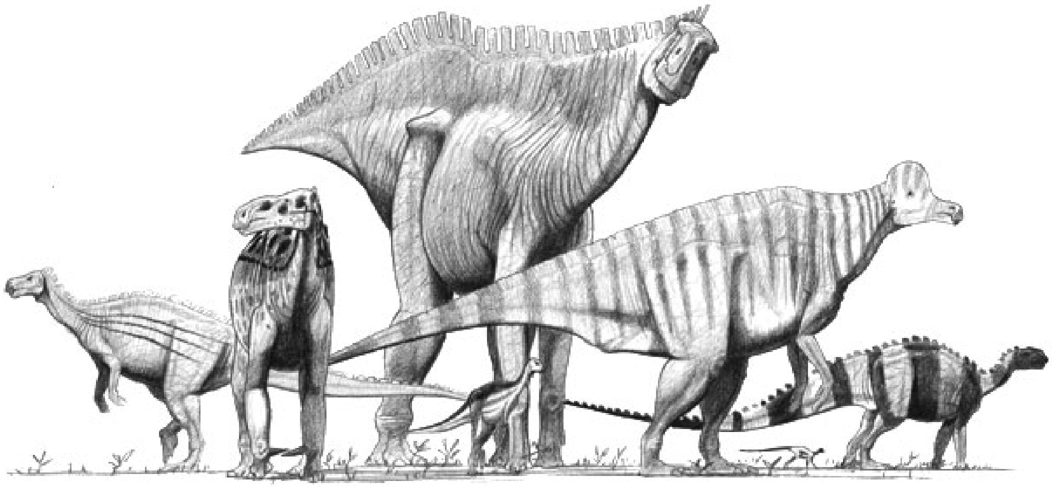
Ornithischian pelvis structure (left side)

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*.

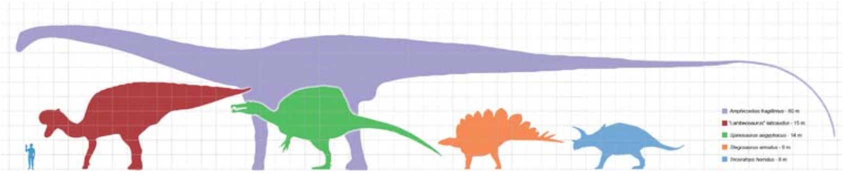
There were three general dinosaur faunas in the Late Cretaceous. In the northern continents of North America and Asia, the major theropods were tyrannosaurids and various types of smaller maniraptoran theropods, with a predominantly ornithischian herbivore assemblage of hadrosaurids, ceratopsians, ankylosaurids, 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



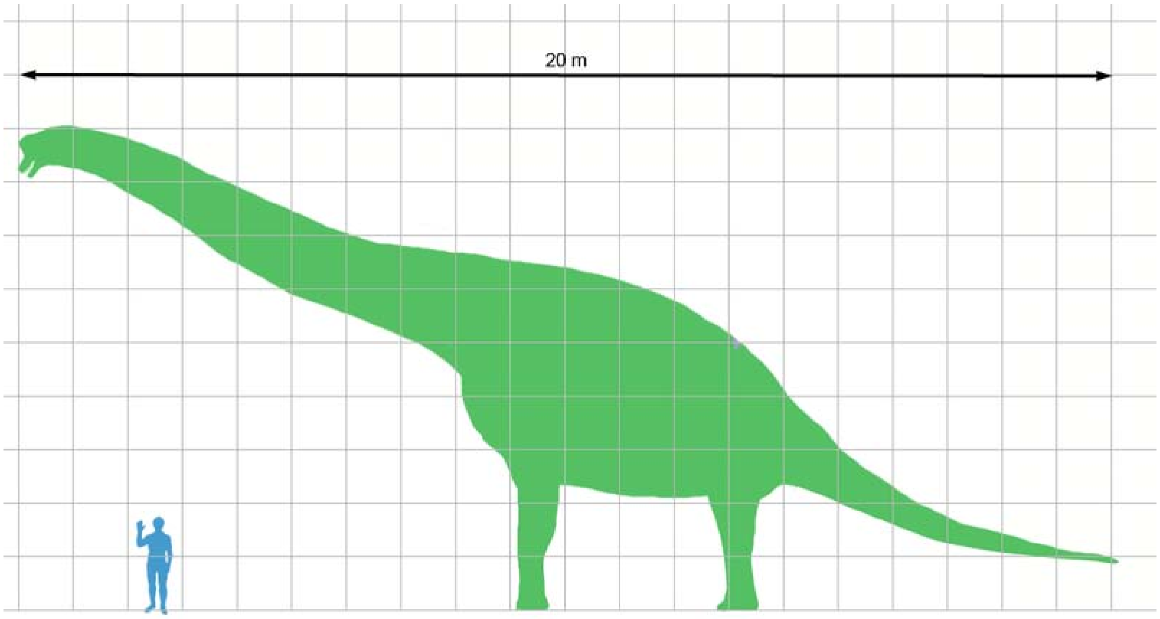
Scale diagram comparing the largest known dinosaurs in five major clades and a human

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).

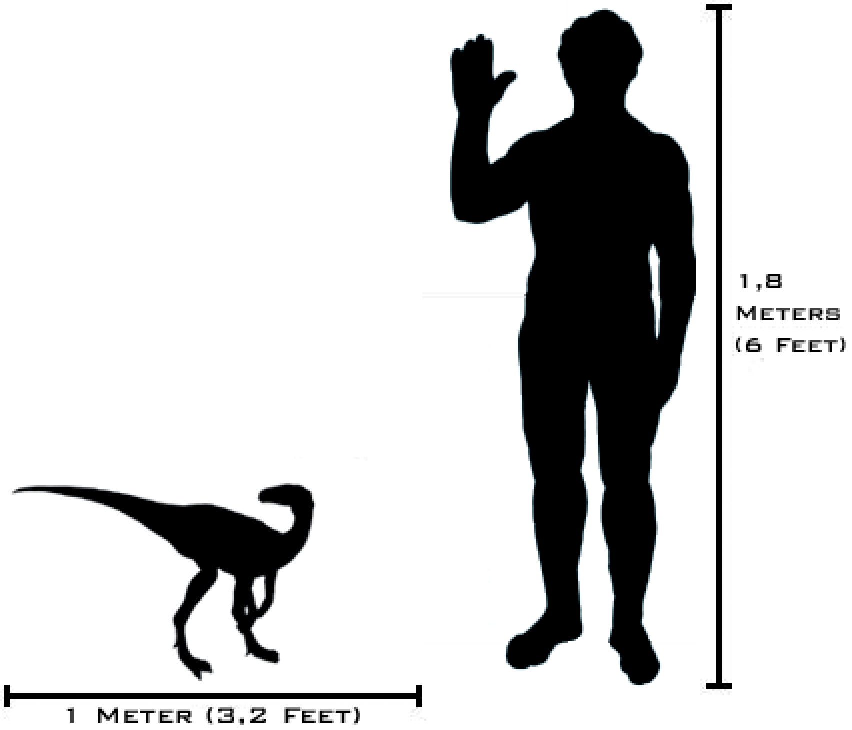
Largest and smallest

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 cords 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 cords, 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*

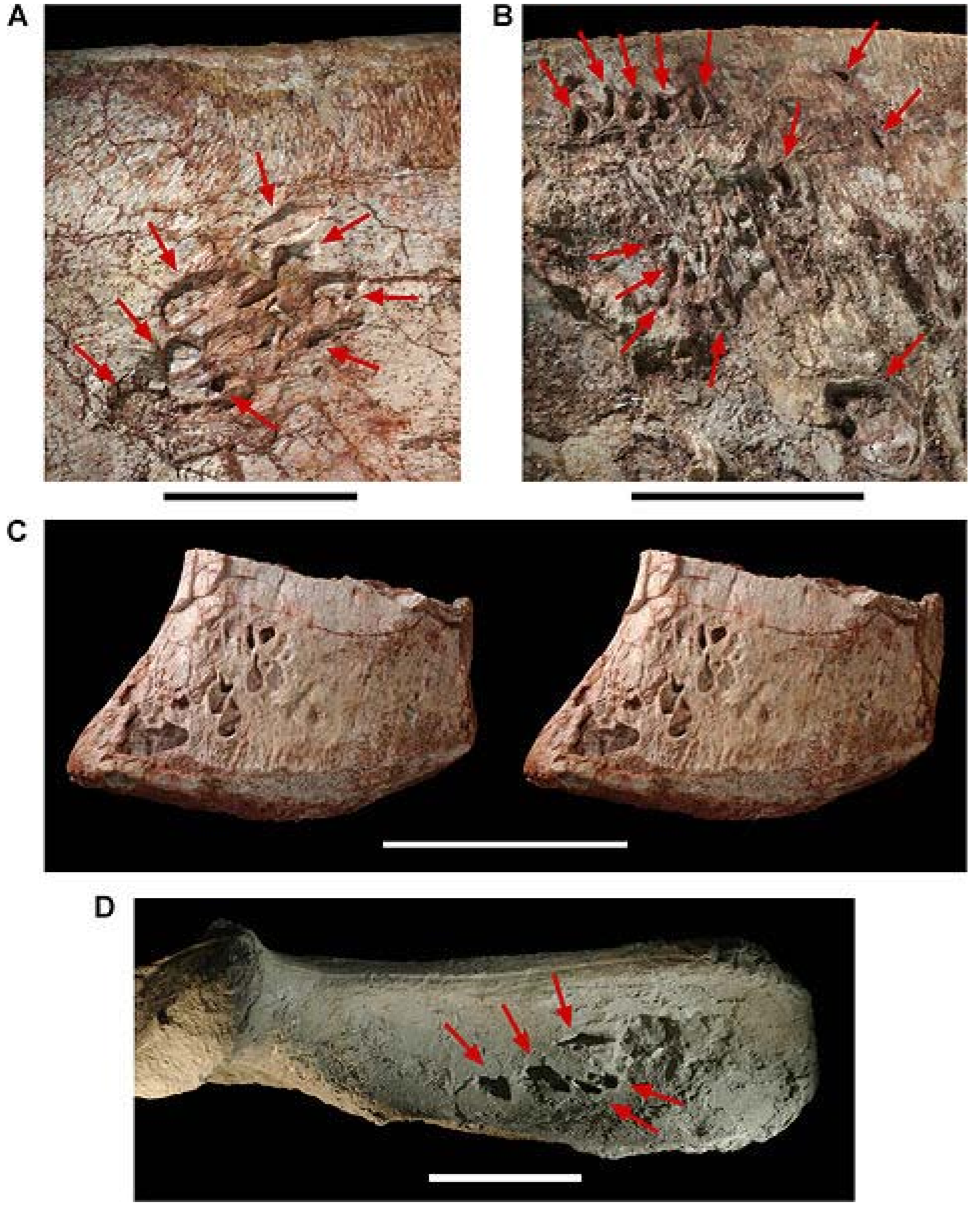
Archaeopteryx, the first good example of a "feathered dinosaur", was discovered in 1861. The initial specimen was found in the Solnhofen limestone in southern Germany, which is a *lagerstätte*, a rare and remarkable geological formation known for its superbly detailed fossils. *Archaeopteryx* is a transitional 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.

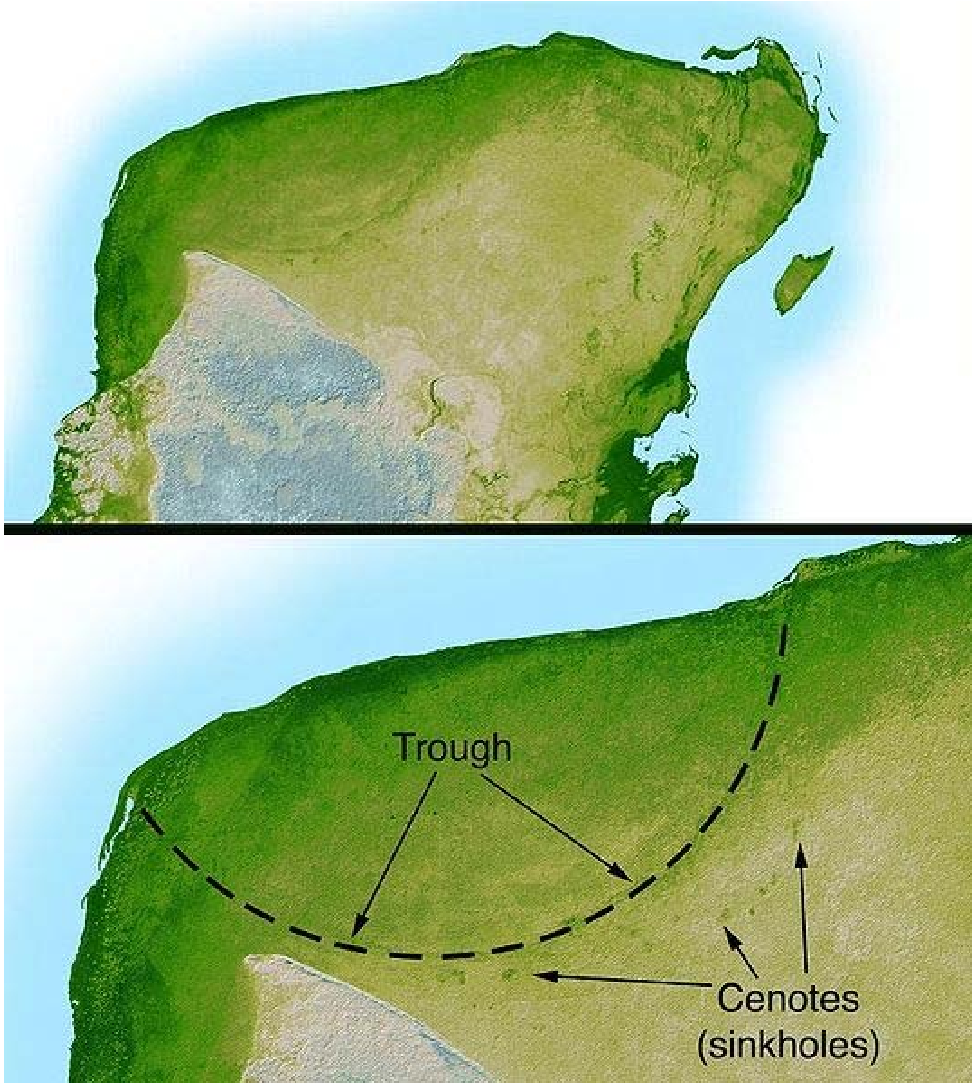
Extinction

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.

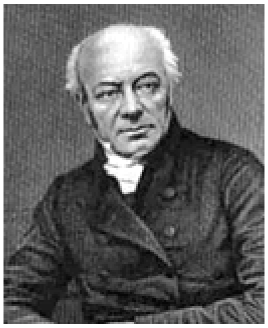
Possible Paleocene survivors

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.



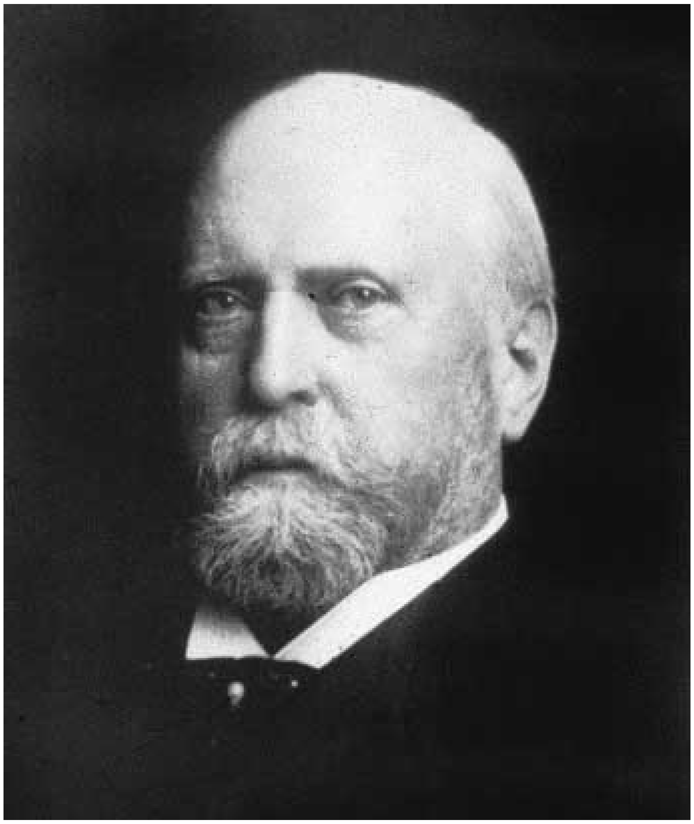
William Buckland

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

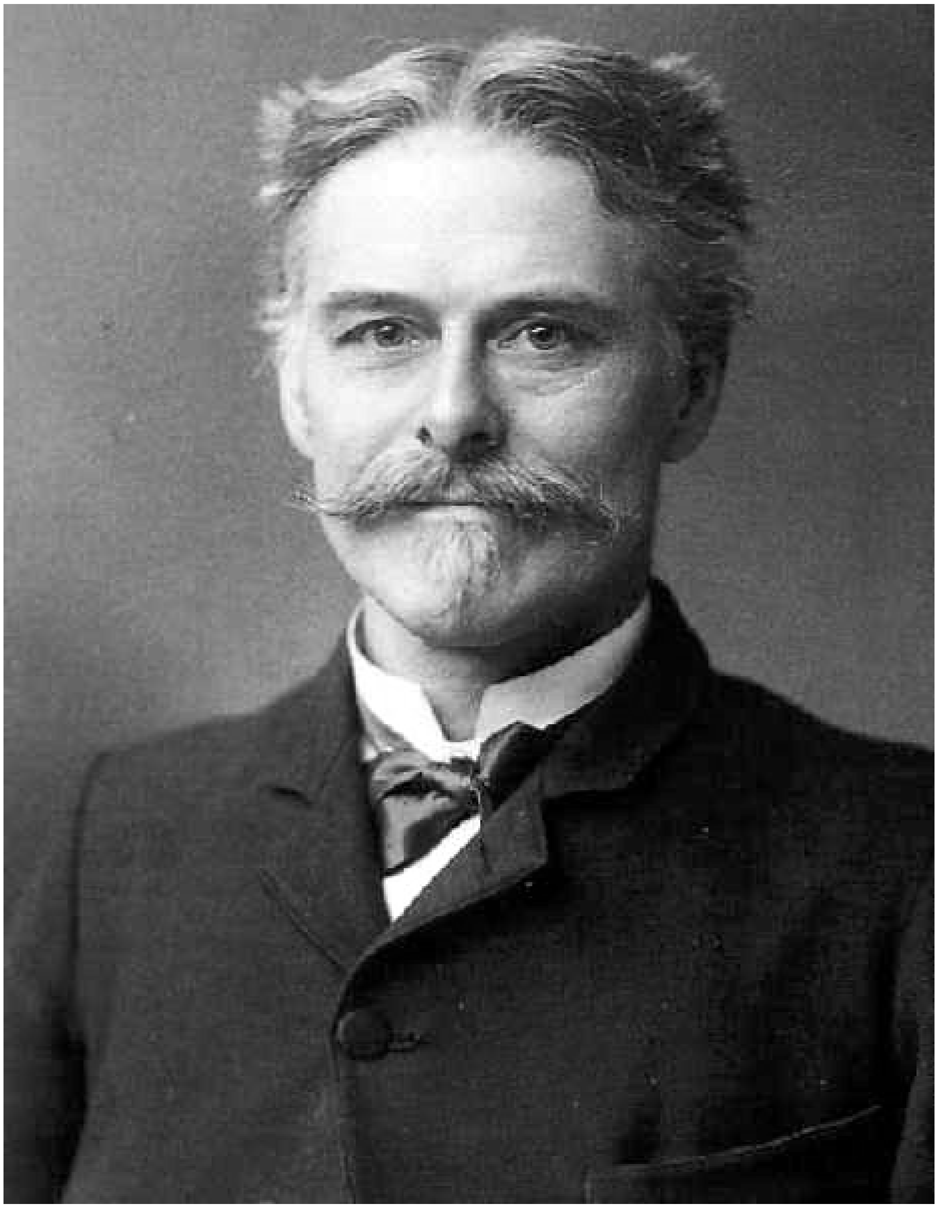
Gideon Mantell. Gideon Mantell recognized similarities between his fossils and the bones of modern iguanas. He published his findings in 1825.

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 3

History of Invertebrate Paleozoology

The **history of invertebrate paleozoology** (also spelled *palaeozoology*) differs from the history of paleontology in that the former usually emphasizes paleobiology and the paleoecology of extinct marine invertebrates, while the latter typically emphasizes the earth sciences and the sedimentary rock remains of terrestrial vertebrates.

The historical development of sub-vertebrate or non-vertebrate paleozoology may also be described as the **history of invertebrate paleobiology** or as the **history of invertebrate paleontology**. Nearly synonymous are the **history of marine paleozoology**, **history of marine paleobiology**, and **history of marine paleontology** -- although the latter three may cover prehistoric fishes, sharks and simpler sea-dwelling organisms.

By far, invertebrate paleozoology is the easiest type of fossil collecting. *Unlike* the difficult-to-analyze and hard-to-interpret fossils of paleobotany (plants) and micropaleontology (microbes), and *unlike* the rarely-found and poorly-preserved skeletons of vertebrate paleontology, invertebrate fossils are usually both common and simple to identify. This is because many prehistoric invertebrates were hard-shelled mollusks, brachiopods, trilobites, bryozoans, crinoids or corals who were buried amid marine, sediment-preserving conditions; and therefore frequently fossilized.

Origins of invertebrate paleozoology

Stone-age people were without doubt the very first fossil collectors. Fossilized echinoderms have been found in Dunstable, Bedfordshire, central England, decorating a long-buried human skeleton; the prehistoric gravesite was Neolithic.

In widely-separated, ancient societies around the globe, there once were many legends and tales of great floods, sea serpents, dragons, sea monsters, and invertebrate cryptozoa associated with so-called *formed stones* or *figured stones* of sea shells, fishes, corals, sea lilies, tracks, burrows, and trails. But, as civilizations progressed, these odd rocks began to be recognized as the fossilized remains and traces of prehistoric animals.

Scholars in ancient Greece produced some of the first scientific insights. Preceding Charles Darwin by two thousand years, Anaximander of Miletus (611 to 547 BCE) proposed a non-creationist, evolutionary theory of life. After Xenophanes of Colophon (576 to 480 BCE) scrutinized fossils of mollusks and other sea-dwelling creatures entombed in rock strata, Xenophanes pronounced that these fossils were evidence of once-living animals. Similarly, after examining fossil sea shells around 440 BCE, Empedocles of Akragas hypothesized that natural selection was occurring over vast, incomprehensible expanses of time.

By the middle of the 4th century BCE, Aristotle was composing *On the Origins of Animals*. Both he and his follower/successor Theophrastus speculated that *plastic forces* within the earth had turned animals into fossils of stone.

Invertebrate paleontology languished for the next two thousand years in medieval Europe, but continued in the medieval Islamic world, with Islamic earth scientists and scholars such as Avicenna (979 to 1039 CE). This Arabic-writing Persian continued the hypothesis that earthen *plastic forces* enabled fossilization. In *The Book of Healing* (1027), Avicenna contributed to paleontology with his explanation of how the stoniness of fossils was caused. Aristotle previously explained it in terms of vaporous exhalations, which Avicenna modified into the theory of petrifying fluids (*succus lapidificatus*), which was elaborated on by Albert of Saxony in the 14th century and accepted in some form by most naturalists by the 16th century. Ibn Sina gave the following explanation for the origin of fossils from the petrifaction of plants and animals:

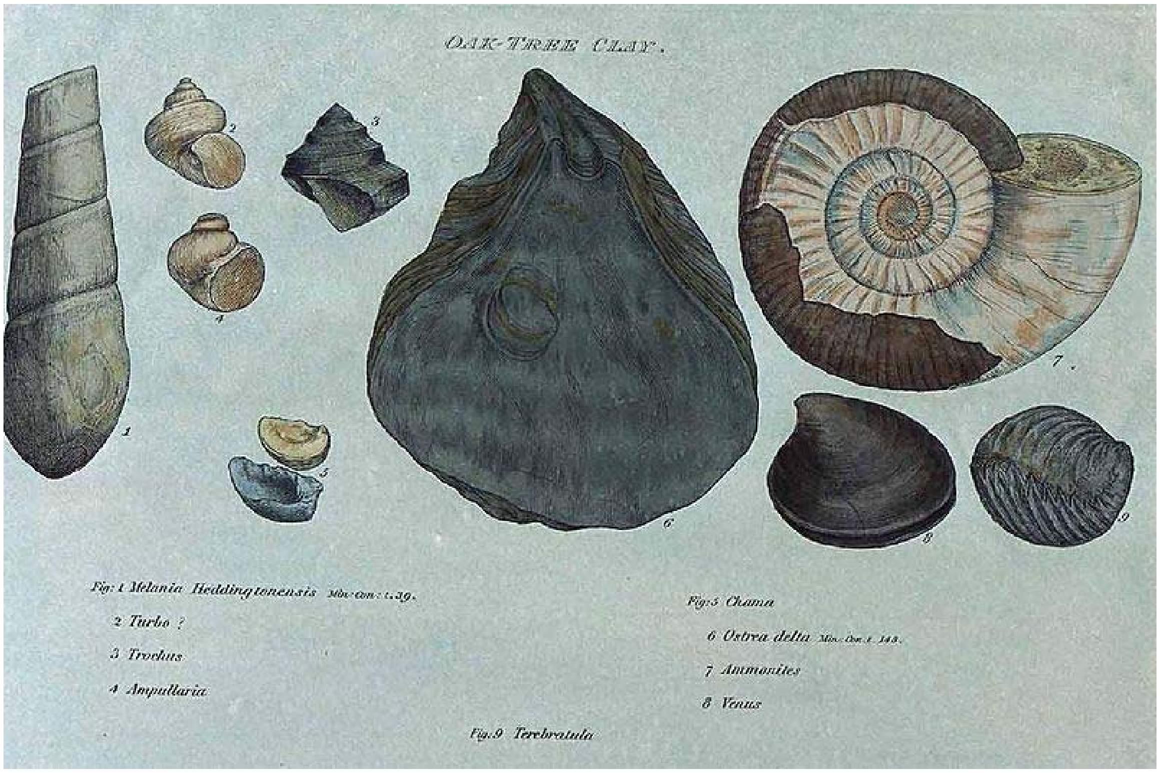
"If what is said concerning the petrifaction of animals and plants is true, the cause of this (phenomenon) is a powerful mineralizing and petrifying virtue which arises in certain stony spots, or emanates suddenly from the earth during earthquake and subsidences, and petrifies whatever comes into contact with it. As a matter of fact, the petrifaction of the bodies of plants and animals is not more extraordinary than the transformation of waters."

The invention of the printing press and the European Renaissance of scientific inquiry (a.k.a. the Age of Reason) changed things. Significantly, Georgius Agricola -- a founder of mineralology -- discussed and illustrated invertebrate fossils in his *De Natura Fossilium* (1546 / 1558).

Although remembered mostly for his development of binomial nomenclature and biotic systematics in his *Systema Naturae* (1735), Carolus Linnaeus also described many prehistoric marine invertebrates which he had observed within Silurian strata in his native Sweden. And while Jean-Étienne Guettard (1715 to 1786) discussed the marine paleoecology of ancient mollusks, more and more fossils were being reported from the Americas and Australasia.

Georges L. L. Buffon subsequently described seven geologic *Epochs of Nature* (1778) wherein he boldly argued that fossiliferous sedimentary strata proved that the world was at least 70,000 years old. In 1795 the very first geochronologic period -- the Jurassic -- was named.

19th century developments



A plate from William Smith's 1815 work *Strata by Organized Fossils*

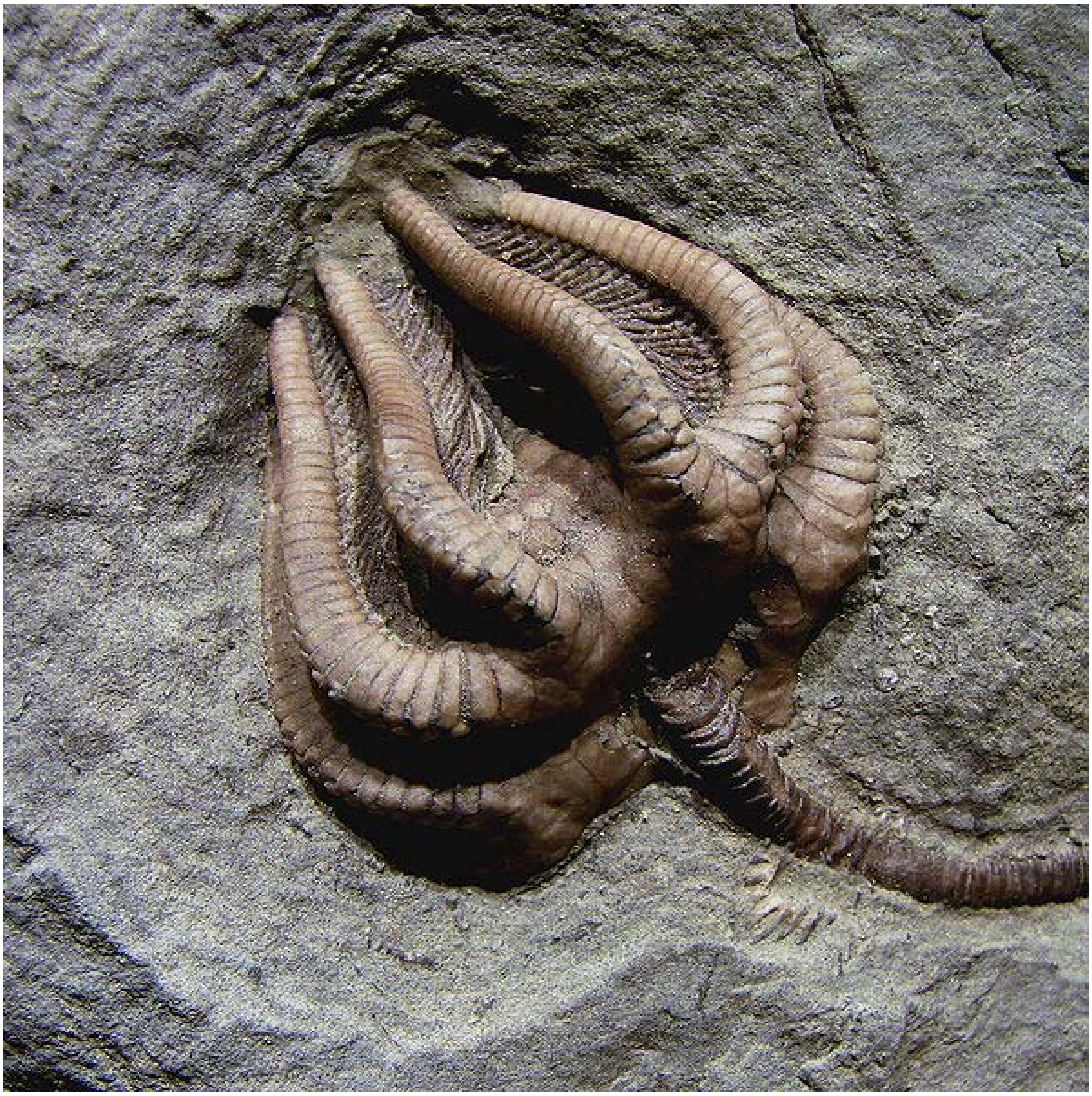
Soon thereafter, Buffon's colleague Chevalier de Lamarck -- a founder of invertebrate systematics and invertebrate paleontology -- published still-more shell fossils in his *Systematics of Animals Without Backbones*, (1801) and his *Natural History of Animals Without Backbones* (1815 to 1822), so as to illustrate global changes in paleogeography. Lamarck also argued that the more adaptable prehistoric invertebrates were the animals that survived environmental change -- a prelude to the concept of *survival of the fittest*.

Next, William Smith employed invertebrate index fossils to map British outcrops in his *Geological Map of England and Wales with Part of Scotland* (1815), and in his book the very next year, *Strata Identified by Organized Fossils* (1816).

Trilobite fossil

Sir Roderick Impey Murchison and Charles Lapworth quarried middle Paleozoic era index fossils, such as the extinct trilobites, extinct graptolites, and mostly-extinct brachiopods. Their efforts led to the latter's ground-breaking treatise, *The Silurian System* (1839), and to the naming of the Ordovician, Silurian, Devonian and Permian geologic periods. Eclipsing Maurchison's inventory of Silurian fossils, however, was Adam Sedgwick's 1835 discovery of even-older Cambrian period fossils. Three years later, Sedgwick proposed that its stratigraphic era be named the Paleozoic.

Meanwhile, yet another Briton, Sir Charles Lyell, penned his *Principles of Geology* (1830) and *Elements of Geology* (1838) in which he divided the Tertiary into the epochs of Eocene, Miocene, Oligocene and Pliocene. By 1834 to 1838, naturalists from France to Russia were using the term "paleontology", and adding yet other names to its prehistoric eons, eras, periods, epochs, and ages.



Crinoid fossil

The provocative *Vestiges of the Natural History of Creation* (1844 to 1853) by then-anonymous Robert Chambers, Alfred Russel Wallace's joint essay (1858) with Charles Darwin, and Darwin's *Origin of Species* (1859 to 1872) popularized the evolutionary theories of natural selection. Indeed, in the very first edition of his *Origin of Species* (1859), Darwin even speculated that the earth might be half a billion years old. Scientific critics, however, pressured him to withdraw this notion from all subsequent editions. In this book Darwin also expressed frustration at the seemingly-total absence of Pre-Cambrian creatures prior to the Cambrian explosion of the invertebrates, since many critics saw this absence as proof of creationism.

Around the same time, James Hall produced his comprehensive, many volumes of *Paleontology of New York* State (1847 to 1894), based on his years of collecting trilobites, graptolites, brachiopods, crinoids, echinoids, mollusks and other ancient marine invertebrates.

Inspired by Darwin's manifesto, Thomas Henry Huxley emphatically cited embryologic and fossil evidence for the evolution of "higher" invertebrates from "lower" cnidarians, worms and mollusks, thereby elaborating what he concluded was *Man's Place in Nature* (1863). Another Darwinist, Ernst Haeckel, proposed a Protozoa-Metazoa theory of animal origins, while arguing that embryonic "ontogeny recapitulates phylogeny" throughout organic prehistory. Haeckel popularized his paleozoologic ideas with majestic genealogical trees of the Animal Kingdom in his *General Morphology of Organisms* (1866).

A half-century later, the genetic conclusions of Gregor Mendel (1822 to 1884) were revived by *The Mutation Theory* propounded by Hugo de Vries, thereby fortifying Darwin's 19th-century theory of evolution.

20th century developments

Around the same time, paleozoologist Charles Doolittle Walcott proved trilobites to be arthropods -- and not at all like mollusks. Then, in 1910, he discovered the *best-preserved* Cambrian fossils ever found: the Burgess shale fauna. Over the next seven years, Walcott excavated 80,000 fossils from the fossiliferous site.

Meanwhile, in *The Origin of Continents and Oceans* (1915 / 1929), Alfred Wegener outlined his heretical theory of continental drift. Although he cited invertebrate fossils and continental geography in support of his idea, another half-century would pass before Wegener's theory would be vindicated by findings in geophysics and plate tectonics.

By that time, 20th-century sciences—such as biometrics, organic chemistry, electron microscopy and molecular phylogenetics -- were aiding invertebrate paleobiologists as they searched for evidence even in the rugged, barren lands of Saharan Africa, Sinkiang, Greater Mongolia, and Antarctica.

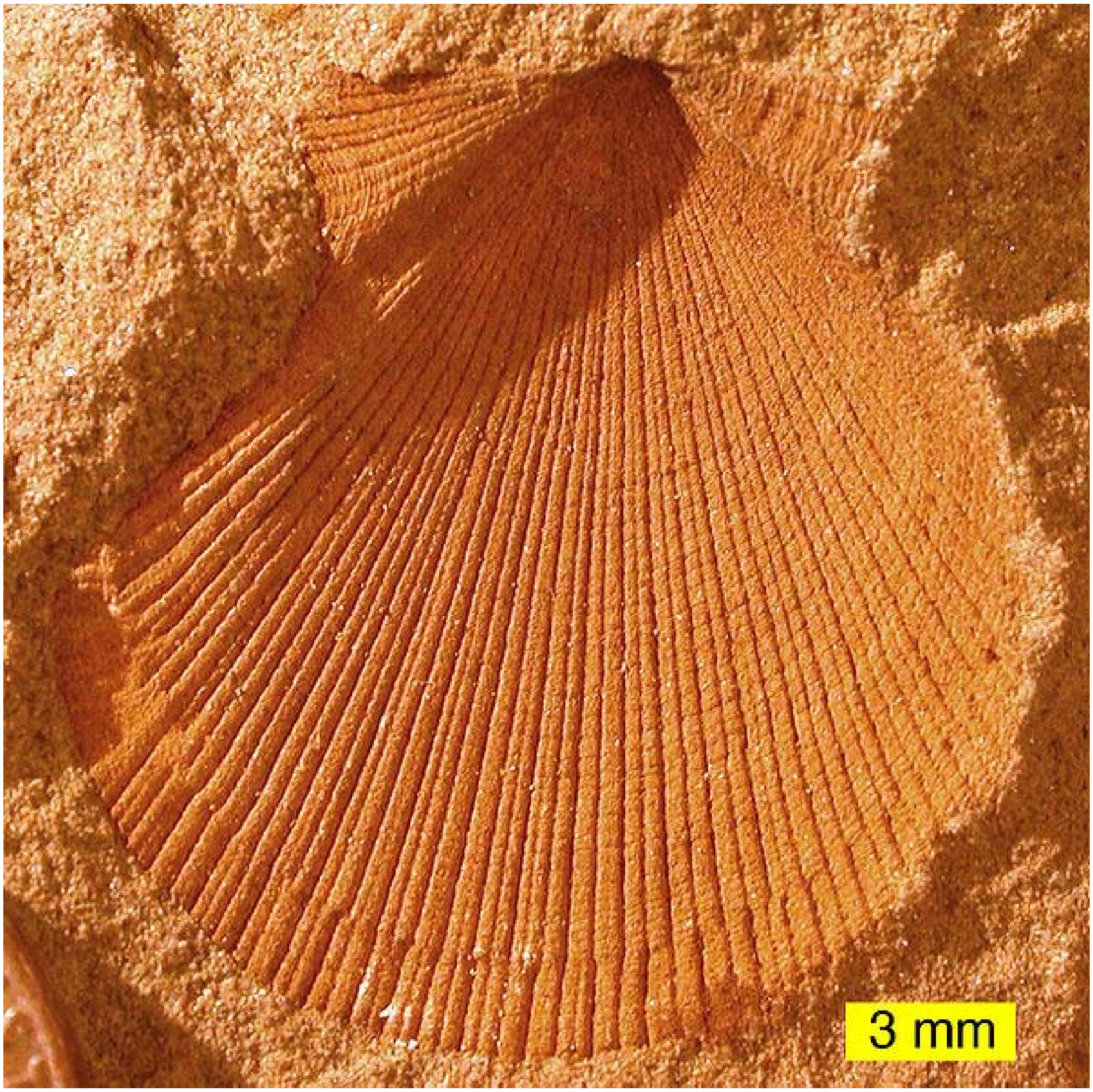
In 1947, paleontologist Reg Sprigg discovered the Ediacaran fauna -- the *best-preserved* fossil invertebrates of the billion-year-long Proterozoic eon. Darwin's 1859 embarrassment at the absence of Pre-Cambrian fossils was now put at rest.

Chapter 4

Invertebrate Paleontology and Odontornithes

Invertebrate paleontology

Bryozoan fossils in an Ordovician oil shale from Estonia. Field of view is 15 cm across.



Aviculopecten subcardiformis; an extinct pectenoid from the Logan Formation (Lower Carboniferous) of Wooster, Ohio (external mold).

Invertebrate paleontology (also spelled **Invertebrate palaeontology**) is sometimes described as **Invertebrate paleozoology** and/or **Invertebrate paleobiology**. Whether it is considered to be a subfield of paleontology, paleozoology, and/or paleobiology, this discipline is the scientific study of **prehistoric invertebrates** by analyzing **invertebrate fossils** in the geologic record.

By *invertebrates* are meant the *non-vertebrate* creatures of the kingdom Animalia (or Metazoa+b vmbnParazoa) in the biotic domain of Eukaryota. By phyletic definition, these many-celled, *sub-vertebrate* animals lack a vertebral column, spinal column, vertebrae, backbone, or long, full-length notochord -- in contrast, of course, to the vertebrates in the one phylum of Chordata.

Relatedly, invertebrates have never had a cartilaginous and/or boney internal skeleton, with its skeletal supports, gill slits, ribs and jaws. Finally, throughout geologic time, invertebrates have remained non-craniate creatures; that is, they never developed a cranium, nerve-chord brain, skull, or hard protective braincase.

Invertebrate terminology in science

In the many decades since Jean-Baptiste de Lamarck, a pioneering biologist and evolutionist, first conceptualized and coined the category "Invertebrata" (between 1793 and 1801) and the term "Biology" (in 1802), zoology has come to recognize that the *non-vertebrate* category is not a scientifically-valid, monophyletic taxon. Evolutionary biology and developmental biology (a.k.a. "evo-devo") now consider the term "Invertebrata" to be both polyphyletic and paraphyletic. Nevertheless, most earth science departments continue to employ this term; and paleontologists find it both useful and practical in evaluating **fossil invertebrates** and—consequently -- **invertebrate evolution**.

However, there is one contemporary caveat: Paleobiologists and microbiologists in the 21st century no longer classify one-celled "animal-like" microbes *either* as invertebrates *or* as animals. For example, the commonly-fossilized foraminifera ("forams") and radiolarians -- zooplankton both formerly grouped under either an animal phylum or animal sub-kingdom called Protozoa ("first animals") -- are now placed in the kingdom or super-kingdom Protista or Protoctista (and thus called *protists* or *protoctists*).

Thus modern **invertebrate paleontologists** deal largely with fossils of this more strictly defined Animal Kingdom (excepting Phylum Chordata), Phylum Chordata being the exclusive focus of vertebrate paleontology. Protist fossils are then the main focus of micropaleontology, while plant fossils are the chief focus paleobotany. Together these four represent the traditional taxonomic divisions of paleontologic study.

Origins and modern evolution of invertebrate paleontology

Invertebrate fossilization

When it comes to the fossil record, *soft*-bodied and *minuscule* invertebrates—such as hydras, jellies, flatworms, hairworms, nematodes, ribbon worms, rotifers and roundworms -- are infrequently fossilized. As a result, paleontologists and other fossil hunters must often rely on trace fossils, microfossils, or chemofossil residue when scouting for these prehistoric creatures.

Hard-bodied and *large* invertebrates are much-more commonly preserved; typically as sizeable macrofossils. These invertebrates are more frequently preserved because their hard parts—for example, shell, armor, plates, tests, exoskeleton, jaws or teeth -- are composed of silica (silicon dioxide), calcite or aragonite (both forms of calcium carbonate), chitin (a protein often infused with tricalcium phosphate), and/or keratin (an even-more complex protein), rather than the vertebrate bone (hydroxyapatite) or cartilage of fishes and land-dwelling tetrapods.

The chitinous jaws of annelids (such as the marine scolecodonts) are sometimes preserved as fossils; while many arthropods and inarticulate brachiopods have easily-fossilized hard parts of calcite, chitin, and/or keratin. The most common and often-found macrofossils are the very hard calcareous shells of articulate brachiopods (that is, the everyday "lampshells") and of mollusks (such as the omnipresent clams, snails, mussels and oysters). On the other hand, non-shelly slugs and non-tubiferous worms (for instance, earthworms) have only occasionally been preserved due to their lack of hard parts.

Odontornithes

Odontornithes is an obsolete and disused taxonomic term proposed by O. C. Marsh for birds possessing teeth, notably the genera *Hesperornis* and *Ichthyornis* from the Cretaceous deposits of Kansas.

In 1875 March divided this "subclass" into **Odontolcae**, with the teeth standing in grooves, and **Odontotormae**, with the teeth in separate alveoles or sockets. In his 1880 work, *Odontornithes: A monograph on the extinct toothed birds of North America*, he added the Saururae, represented by *Archaeopteryx*, as a third order.

The resulting classification was paraphyletic, not accurately resolving evolutionary relationships. In the present case, the Odontornithes are not a monophyletic assembly, and the fact of their possessing teeth proves nothing but that some birds still retained these organs during the Late Cretaceous. This indicates that birds, as a group, are the descendants of toothed reptiles, to the exclusion of the Chelonia (turtles and tortoises) with which various authors had attempted to connect them. No fossil birds of later than Cretaceous age are known to have teeth.

Étienne Geoffroy Saint-Hilaire stated in 1821 that he had found a considerable number of tooth buds in the upper and lower jaws of the Rose-ringed Parakeet. Émile Blanchard felt justified in recognizing flakes of dentine. However, M. Braun and especially P. Fraisse showed later that the structures in question are of the same kind as the well-known serrated " teeth " of the bill of anserine birds. In fact the papillae observed in the embryonic birds are the soft cutaneous extensions into the surrounding horny sheath of the bill, comparable to the well-known nutritive papillae in a horse's hoof. They are easily exposed in the well-macerated under jaw of a parrot, after removal of the horny sheath. Occasionally calcification occurs in or around these papillae, as it does regularly in the egg tooth of the embryos of all birds.

The best known of the "Odontornithes" are *Hesperornis regalis*, standing about 3ft. high, the somewhat taller *H. crassipes*, and *Ichthyornis dispar*. *Hesperornis* looked somewhat similar to a loon, while *Ichthyornis* was quite similar to a gull or petrel. However, they were entirely distinct groups of birds and merely shared with modern birds some distant ancestry in the Early Cretaceous. The *Hesperornis* lineage may have derived even sooner or possibly independently from the ancestors of modern birds.

Chapter 5

Scolecodont and Vertebrate Paleontology

Scolecodont

An Ordovician scolecodont from Estonia

A **scolecodont** is the jaw of a **polychaete** annelid, a common type of fossil-producing segmented worm useful in invertebrate paleontology. **Scolecodonts** are common and diverse microfossils, which range from the Cambrian period (around half a billion years ago at the start of the Paleozoic era) to the present. They diversified profusely in the Ordovician, and are most common in the Ordovician, Silurian and Devonian marine deposits of the Paleozoic era.

Relatedly, more problematic worm-like fossils have been described in even older, Neoproterozoic era deposits in the Ediacaran Hills of southern Australia and in mid-Cambrian deposits of Burgess shale in British Columbia.

Since the other classes of annelids (specifically, the earthworms and leeches) lack hard parts, only the sea-dwelling **polychaetes** are frequently represented in the fossil record. Polychaetes are commonly fossilized due to their chitinous teeth and their dwelling tubes made of durable calcite (a calcium carbonate), hardened mucus (a.k.a. parchment), and/or chitin-like cement.

Scolecodonts belonging to the extinct families Atraktoprionidae, Hadoprionidae, Kalloprionidae, Mochtyellidae, Paulinitidae, Polychaetaspidae, Ramphoprionidae, Rhytiprionidae, Skalenoprionidae, Symmetroprionidae, Xanioprionidae, and the still-extant (living) family Oenonidae (which includes the Arabellidae) are known from Silurian rocks in Scotland. Scolecodonts representing the present-day families Onuphidae and Dorvilleidae first appeared in Mesozoic era deposits.

Vertebrate paleontology

Vertebrate paleontology seeks to discover the behavior, reproduction and appearance of extinct animals with vertebrae or a notochord, through the study of their fossilized remains. It also tries to connect, by using the evolutionary timeline, the animals of the past and their modern-day relatives.

The fossil record does not clearly show the evolutionary progression from early aquatic vertebrates to mammals, but there is some evidence. The earliest known fossil vertebrates were heavily armored fish discovered in rocks from the Ordovician Period about 500 to 430 Ma (megaannum, million years ago). The Devonian Period (395 to 345 Ma) brought in the changes that allowed primitive air-breathing fish to remain on land as long as they wished, thus becoming the first terrestrial vertebrates, the amphibians.

Amphibians developed forms of reproduction and locomotion and a metabolism better suited for life exclusively on land, becoming more reptilian. Full fledged reptiles appeared in the Carboniferous Period (345 to 280 Ma).

The reptilian changes and adaptations to diet and geography are chronicled in the fossil record of the varying forms of therapsida. True mammals showed up in the Triassic

Period (225 to 190 Ma) around the same time as the dinosaurs, which also sprouted from the reptilian line.

Birds first diverged from dinosaurs between 100 Ma and 60 Ma .

History

One of the people who helped figure out the vertebrate progression was French zoologist Georges Cuvier (1769-1832), who realized that fossils found in older rock strata differed greatly from more recent fossils or modern animals. He published his findings in 1812 and, although he steadfastly refuted evolution, his work proved the (at the time) contested theory of extinction of species.

Thomas Jefferson is credited with initiating the science of vertebrate paleontology in the United States with the reading of a paper to the American Philosophical Society in Philadelphia in 1797. Jefferson presented fossil bones of a ground sloth found in a cave in western Virginia and named the genus (*Megalonyx*). The species was ultimately named *Megalonyx jeffersonii* in his honor. Jefferson corresponded with Cuvier, including sending him a shipment of highly desirable bones of the American mastodon and the woolly mammoth.

Paleontology really got started though, with the publication of *Recherches sur les poissons fossils* (1833-1843) by Swiss naturalist Louis Agassiz (1807-1873). He studied, described and listed hundreds of species of fossil fish, beginning the serious study into the lives of extinct animals.

In modern times, some have said that Alfred Romer (1894-1973) wrote the definitive textbook on the subject, called *Vertebrate Paleontology*, which shows the progression of evolution in fossil fish, and amphibians and reptiles through comparative anatomy. Romer became the first president of the Society of Vertebrate Paleontology in 1940, alongside co-founder Howard Chiu. Others would claim that the current definitive book on the subject was written by Robert L. Carroll of McGill University in his 1988 text *Vertebrate Paleontology and Evolution*. Carroll was president of the Society of Vertebrate Paleontology in 1983. The Society keeps its members informed on the latest discoveries through newsletters and the *Journal of Vertebrate Paleontology*.

Paleontological Vertebrate Classification

This is a 'traditional' classification scheme, which can technically be described as paraphyletic. This means that the classification scheme does not necessarily represent the evolutionary history of the classes. For instance, birds are generally considered to be the descendants of Saurischian dinosaurs, but in this system both are listed as separate classes.

Kingdom Animalia

- Phylum Chordata (vertebrates)
    - Class Agnatha (jawless fish)
    - Class Placodermi (armored fish)
    - Class Chondrichthyes (sharks)
    - Class Osteichthyes (bony fish)
    - Class Amphibia
    - Class Reptilia
        - Subclass Anapsida
            - Order Cotylosauria
            - Order Chelonia
        - Subclass Synapsida
            - Order Pelycosauria
            - Order Therapsida
        - Subclass Euryapsida
            - Order Sauropterygia
            - Order Ichthyosauria
        - Subclass Diapsida (lizards & snakes too)
            - Order Crocodilia (crocodiles, alligators etc)
            - Order Thecodonts
            - Order Pterosauria
            - Order Saurischia (dinosaurs)
            - Order Ornithischia (dinosaurs)

- Class Aves
- Class Mammalia

- Subclass Prototheria
    - Order Monotremata (platypus and the echidnas)
- Subclass Theria
    - Infraclass Metatheria
        - Order Marsupialia (kangaroos, dunnarts, opposums, wombats etc)
    - Infraclass Eutheria (placentals)
        - Order Insectivora
        - Order Chiroptera (bats)
        - Order Creodonta
        - Order Carnivora (dogs/cats)
        - Order Perissodactyla (horses)
        - Order Artiodactyla (cattle and other ungulates)
        - Order Proboscidea (elephants)
        - Order Edentata
        - Order Cetacea (whales and dolphins)
        - Order Rodentia (mice, rats etc)
        - Order Lagomorpha (rabbits)
        - Order Primates (monkeys, apes and primates)

Chapter 6

Trace fossil

Chirotherium footprints in a Triassic sandstone.

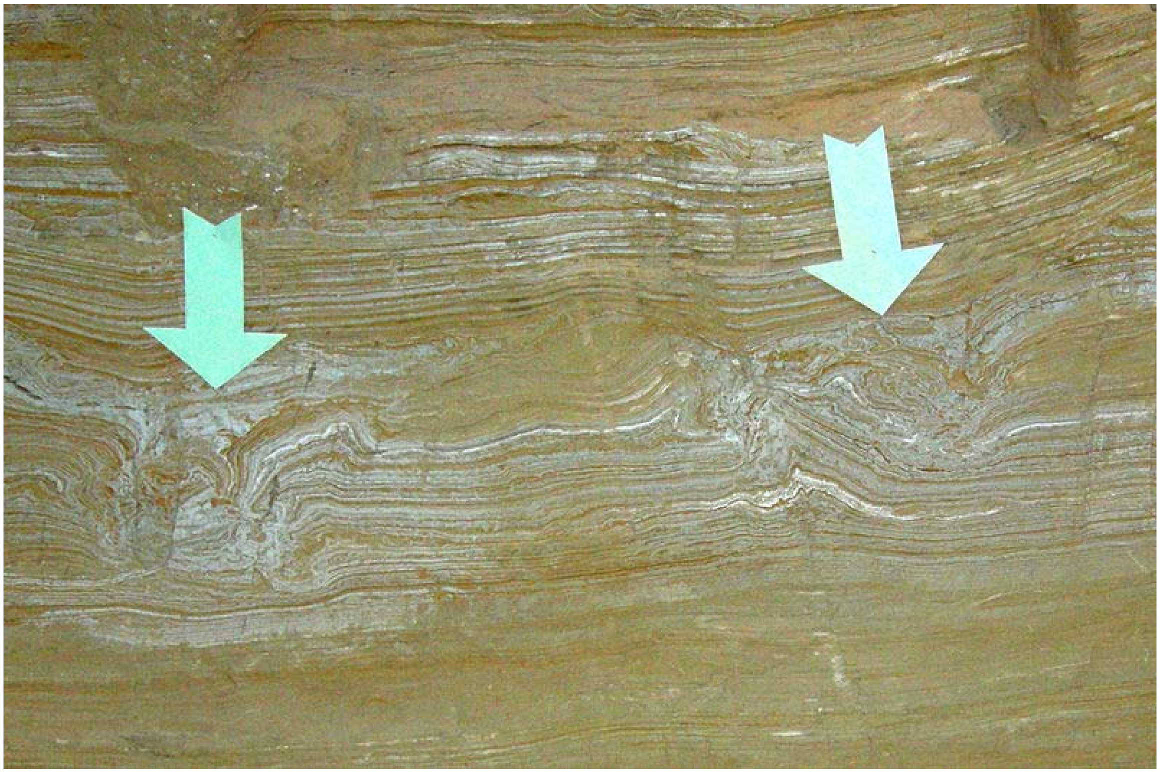
Protichnites tracks from the late Cambrian, central Wisconsin.

Trace fossils, also called **ichnofossils** are geological records of biological activity. Trace fossils may be impressions made on the substrate by an organism: for example, burrows, borings (bioerosion), urolites (erosion caused by evacuation of liquid wastes), footprints and feeding marks, and root cavities. The term in its broadest sense also includes the remains of other organic material produced by an organism — for example coprolites (fossilized droppings) or chemical markers — or sedimentological structures produced by biological means - for example, stromatolites. Trace fossils contrast with body fossils, which are the fossilized remains of parts of organisms' bodies, usually altered by later chemical activity or mineralization.

Sedimentary structures, for example those produced by empty shells rolling along the sea floor, are not produced through the behaviour of an organism and not considered trace fossils.

The study of traces is called ichnology, which is divided into *paleoichnology*, or the study of trace fossils, and *neoichnology*, the study of modern traces. This science is challenging, as most traces reflect the behaviour — not the biological affinity — of their makers. As such, trace fossils are categorised into form genera, based upon their appearance and the implied behaviour of their makers.

Occurrence



Cross-section of mammoth footprints at The Mammoth Site, Hot Springs, South Dakota.

Traces are better known in their fossilised form than in modern sediments. This makes it difficult to interpret some fossils by comparing them with modern traces, even though they may be extant or even common. The main difficulties in accessing extant burrows stem from finding them in consolidated sediment, and being able to access those formed in deeper water.

Trace fossils are best preserved in sandstones; the grain size and depositional facies both contributing to the better preservation. They may also be found in shales and limestones.

Classification

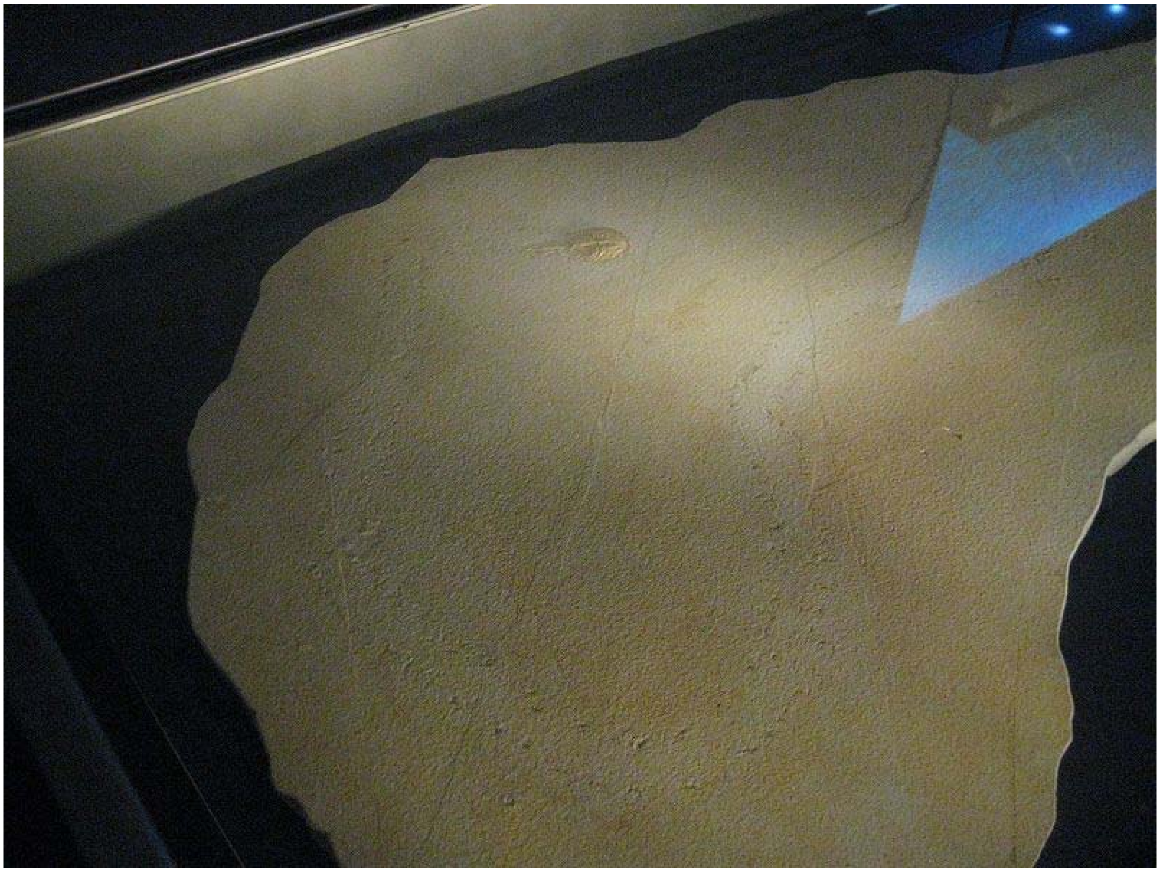
Trace fossils are generally difficult or impossible to assign to a specific maker. Only in very rare occasions are the makers found in association with their tracks. Further, entirely different organisms may produce identical tracks. Therefore conventional taxonomy is not applicable, and a comprehensive form taxonomy has been erected. At the highest level of the classification, five behavioral modes are recognized:

- **Domichnia**, dwelling structures reflecting the life position of the organism that created it.
- **Fodinichnia**, three-dimensional structures left by animals which eat their way through sediment, such as deposit feeders;

- **Pascichnia**, feeding traces left by grazers on the surface of a soft sediment or a mineral substrate;
- **Cubichnia**, resting traces, in the form of an impression left by an organism on a soft sediment;
- **Repichnia**, surface traces of creeping and crawling.

Fossils are further classified into form genera, a few of which are even subdivided to a "species" level. Classification is based on shape, form, and implied behavioural mode.

Information provided by ichnofossils



Mesolimulus walchi fossil and track, a rare example of tracks and the creature that made them fossilized together

Because identical fossils can be created by a range of different organisms, trace fossils can only reliably inform us of two things: the consistency of the sediment at the time of its deposition, and the energy level of the depositional environment. Attempts to deduce such traits as whether a deposit is marine or non-marine have been made, but shown to be unreliable.

Paleoecology

Trace fossils provide us with indirect evidence of life in the past, such as the footprints, tracks, burrows, borings, and feces left behind by animals, rather than the preserved remains of the body of the actual animal itself. Unlike most other fossils, which are produced only after the death of the organism concerned, trace fossils provide us with a record of the activity of an organism during its lifetime.

Trace fossils are formed by organisms performing the functions of their everyday life, such as walking, crawling, burrowing, boring, or feeding. Tetrapod footprints, worm trails and the burrows made by clams and arthropods are all trace fossils.

Perhaps the most spectacular trace fossils are the huge, three-toed footprints produced by dinosaurs and related archosaurs. These imprints give scientists clues as to how these animals lived. Although the skeletons of dinosaurs can be reconstructed, only their fossilized footprints can determine exactly how they stood and walked. Such tracks can tell much about the gait of the animal which made them, what its stride was, and whether or not the front limbs touched the ground.

However, most trace fossils are rather less conspicuous, such as the trails made by segmented worms or nematodes. Some of these worm castings are the only fossil record we have of these soft-bodied creatures.

Paleoenvironment

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

Fossil footprints made by tetrapod vertebrates are difficult to identify to a particular species of animal, but they can provide us with valuable information such as the speed, weight, and behavior of the organism that made them. Such trace fossils are formed when amphibians, reptiles, mammals or birds walked across soft (probably wet) mud or sand which later hardened sufficiently to retain the impressions before the next layer of sediment was deposited. Some fossils can even provide details of how wet the sand was when they were being produced, and hence allow estimation of paleo-wind directions.

Assemblages of trace fossils occur at certain water depths, and can also reflect the salinity and turbidity of the water column.

Stratigraphic correlation

Some trace fossils can be used as local index fossils, to date the rocks in which they are found, such as the burrow *Arenicolites franconicus* which occurs only in a 4 cm (1.6") layer of the Triassic Muschelkalk epoch, throughout wide areas in southern Germany.

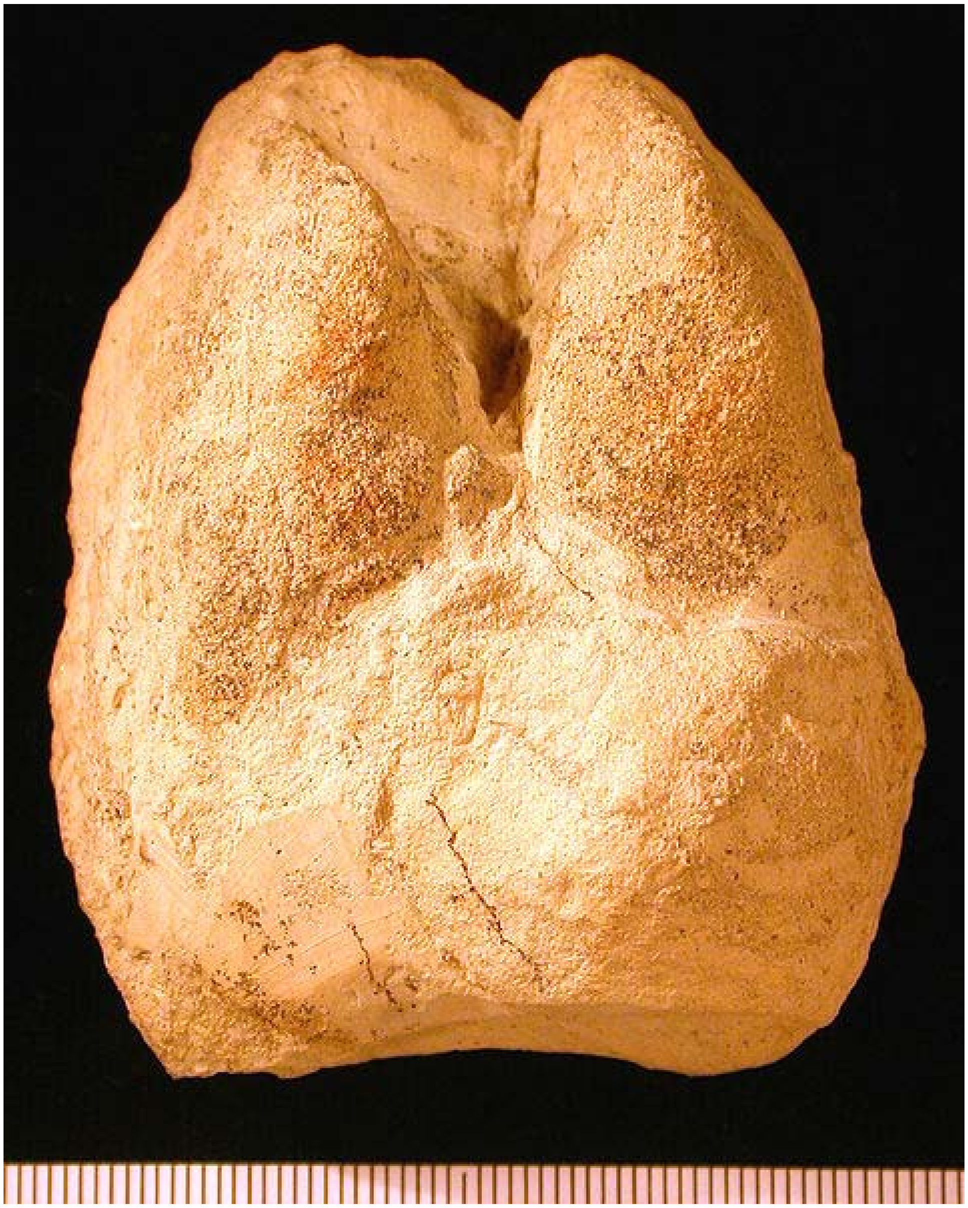
The base of the Cambrian period is defined by the first appearance of the trace fossil *Treptichnus pedum*.

Trace fossils have a further utility as many appear before the organism thought to create them, extending their stratigraphic range.

Ichnofacies

Trace fossil assemblages are far from random; the range of fossils recorded in association is constrained by the environment in which the trace-making organisms dwelt. Palaeontologist Adolf Seilacher pioneered the concept of ichnofacies, whereby the state of a sedimentary system at its time of deposition could be implied by noting the fossils in association with one another.

Inherent bias



Cameloid footprint (convex hyporelief) from the Barstow Formation (Miocene) of Rainbow Basin, California.

Most trace fossils are known from marine deposits. Essentially, there are two types of traces, either exogenic ones, which are made on the surface of the sediment (such as tracks) or endogenic ones, which are made within the layers of sediment (such as burrows).

Surface trails on sediment in shallow marine environments stand less chance of fossilization because they are subjected to wave and current action. Conditions in quiet, deep-water environments tend to be more favorable for preserving fine trace structures.

Most trace fossils are usually readily identified by reference to similar phenomena in modern environments. However, the structures made by organisms in recent sediment have only been studied in a limited range of environments, mostly in coastal areas, including tidal flats.

Evolution

Climactichnites, probably trackways from a slug-like animal, from the late Cambrian, central Wisconsin. *Ruler in background is 45cm (18") long.*

The earliest complex trace fossils, not including microbial traces such as stromatolites, date to 2,000 to 1,800 million years ago. This is far too early for them to have an animal origin, and they are thought to have been formed by amoedae. Putative "burrows" dating as far back as 1,100 million years may have been made by animals which fed on the undersides of microbial mats, which would have shielded them from a chemically unpleasant ocean; however their uneven width and tapering ends make a biological origin so difficult to defend that even the original author no longer believes they are authentic.

The first evidence of burrowing which is widely accepted dates to the Ediacaran (Vendian) period, around 560 million years ago. During this period the traces and burrows basically are horizontal on or just below the seafloor surface. Such traces must have been made by motile organisms with heads, which would probably have been bilateran animals. The trace observed imply simple behaviour, and point to organisms feeding above the surface and burrowing for protection from predators. Contrary to widely circulated opinion that Ediacaran burrows are only horizontal the vertical burrows *Skolithos* are also known. The producers of burrows *Skolithos declinatus* from the Vendian (Ediacaran) beds in Russia with date 555.3 million years ago have not been found, they might have been filter feeders subsisting on the nutrients from the suspension. The density of these burrows is up to 245 burrows/dm^2. Some Ediacaran trace fossils have been found directly associated with an body fossils. *Yorgia* and *Dickinsonia* are often found at the end of long pathways of trace fossils matching their shape. The feeding was performed in a mechanical way, supposedly the ventral side of body these organisms was covered with cilia. The potential mollusc related *Kimberella* is associated with scratch marks, perhaps formed by a radula, further traces from 555 million years ago appear to imply active crawling or burrowing activity.

As the Cambrian got underway, new forms of trace fossil appeared, including vertical burrows (e.g. *Diplocraterion*) and traces normally attributed to arthropods. These represent a “widening of the behavioural repertoire”, both in terms of abundance and complexity.

Trace fossils are a particularly significant source of data from this period because they represent a data source that is not directly connected to the presence of easily-fossilized hard parts, which are rare during the Cambrian. Whilst exact assignment of trace fossils to their makers is difficult, the trace fossil record seems to indicate that at the very least, large, bottom-dwelling, bilaterally symmetrical organisms were rapidly diversifying during the early Cambrian.

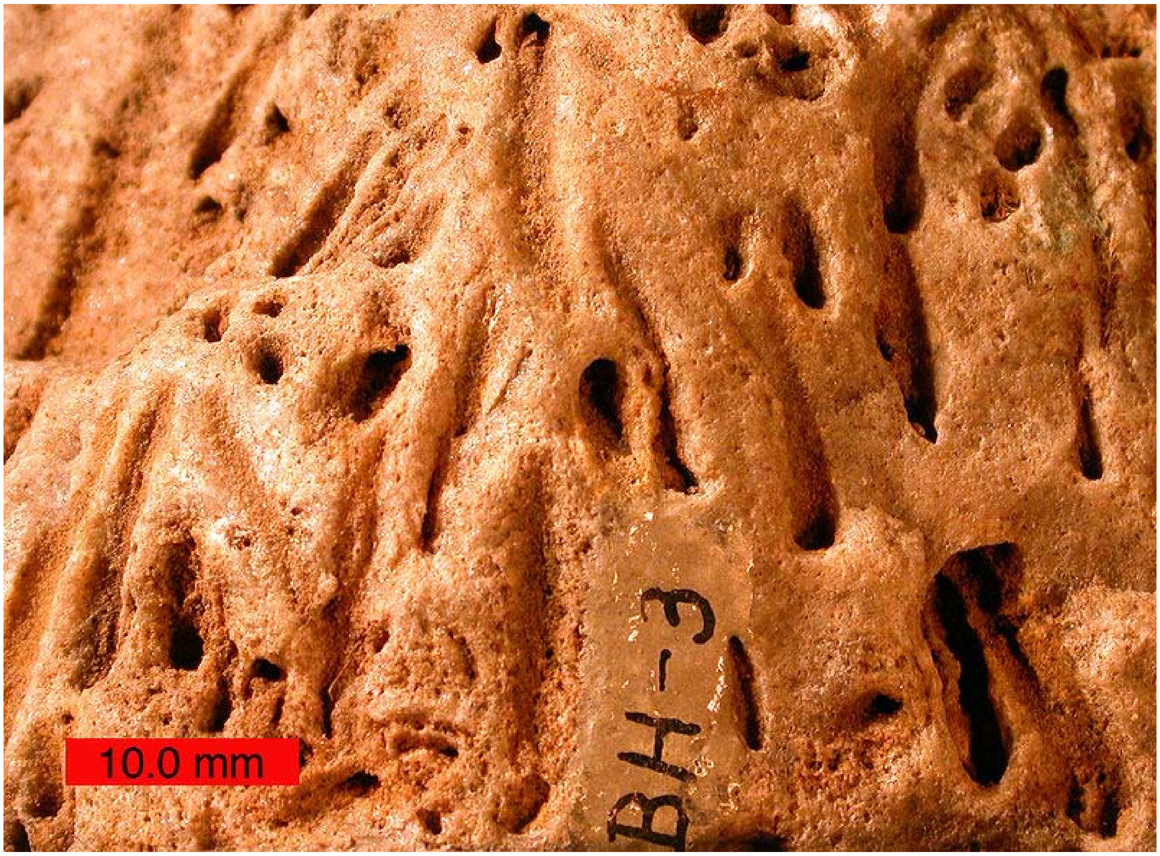
Further, less rapid diversification occurred since, and many traces have been converged upon independently by unrelated groups of organisms.

Trace fossils also provide our earliest evidence of animal life on land. The earliest arthropod trackways date to the Cambro-Ordovician, and trackways from the Ordovician Tumblagooda sandstone allow the behaviour of these organisms to be determined. The enigmatic trace fossil *Climactichnites* may represent an earlier still terrestrial trace, perhaps made by a slug-like organism.

Common ichnogenera

Petroxestes borings in a hardground from the Upper Ordovician of southern Ohio.

Rusophycus trace fossil from the Ordovician of southern Ohio. Scale bar is 10 mm.



Skolithos trace fossil. Scale bar is 10 mm.

Thalassinoides, burrows produced by crustaceans, from the Middle Jurassic, Makhtesh Qatan, southern Israel.

Trypanites borings in an Upper Ordovician hardground from northern Kentucky. The borings are filled with diagenetic dolomite (yellowish). Note that the boring on the far right cuts through a shell in the matrix.

- *Asteriacites* is the name given to the five-rayed fossils found in rocks and they record the resting place of starfish on the sea floor. *Asteriacites* are found in European and American rocks, from the Ordovician period onwards, and are numerous in rocks from the Jurassic period of Germany.
- *Chondrites* (not to be confused with stony meteorites of the same name) are small branching burrows of the same diameter, which superficially resemble the roots of a plant. The most likely candidate for having constructed these burrows is a nematode (roundworm). *Chondrites* are found in marine sediments from the Cambrian period of the Paleozoic onwards. They are especially common in sediments which were deposited in reduced-oxygen environments.
- *Climactichnites* is the name given to trackways that usually consist of two parallel ridges separated by chevron-shaped raised cross bars. They somewhat resemble tire tracks, and are larger (typically about four inches wide) than most of the other trace fossils made by invertebrates. The tracks were produced on sandy tidal flats during late Cambrian time. While the identity of the animal is still conjectural, it may have been a large slug-like animal - its trackways produced as it crawled over and processed the wet sand to obtain food.
- *Cruziana* are excavation trace marks made on the sea floor which have a two-lobed structure with a central groove. The lobes are covered with scratch marks made by the legs of the excavating organism, usually a trilobite or allied arthropod. *Cruziana* are most common in marine sediments formed during the Paleozoic era, particularly in rocks from the Cambrian and Ordovician periods. Over 30 ichnospecies of *Cruziana* have been identified..
- *Entobia* is a boring produced by endolithic clionaid sponges consisting of galleries excavated in a carbonate substrate; often has swollen chambers with connecting canals.
- *Gastrochaenolites* are clavate (club-shaped) borings also produced in calcareous hard substrates, usually by bivalves.
- *Petroxestes* is a shallow groove boring produced by mytilacean bivalves in carbonate hard substrates.
- *Protichnites* consists of two rows of tracks and a linear depression between the two rows. The tracks are believed to have been made by the walking appendages of arthropods. The linear depression is thought to be the result of a dragging tail. The structures bearing this name were typically made on the tidal flats of Paleozoic seas, but similar ones extend into the Cenozoic.
- *Rhizocorallium* is a type of burrow, the inclination of which is typically within 10° of the bedding planes of the sediment. These burrows can be very large, over a meter long in sediments that show good preservation, e.g. Jurassic rocks of the Yorkshire Coast (eastern United Kingdom), but the width is usually only up to 2 cm, restricted by the size of the organisms producing it. It is thought that they represent fodinichnia as the animal (probably a nematode) scoured the sediment for food.
- *Rogerella* is a small pouch-shaped boring with a slit-like aperture currently produced by acrothoracican barnacles.
- *Rusophycus* are bilobed "resting traces" associated with trilobites and other arthropods such as horseshoe crabs.

- *Skolithos*: One well-known occurrence of Cambrian trace fossils from this period is the famous 'Pipe Rock' of northwest Scotland. The 'pipes' that give the rock its name are closely packed straight tubes- which were presumably made by some kind of worm-like organism. The name given to this type of tube or burrow is *Skolithos*, which may be 30 cm (12") in length and between 2 to 4 cm (0.8 to 1.6") in diameter. Such traces are known worldwide from sands and sandstones deposited in shallow water environments, from the Cambrian period (542–488 Ma) onwards.
- *Thalassinoides* are burrows which occur parallel to the bedding plane of the rock and are extremely abundant in rocks, worldwide, from the Jurassic period onwards. They are repeatedly branched, with a slight swelling present at the junctions of the tubes. The burrows are cylindrical and vary from 2 to 5 cm (0.8" to 2") in diameter. *Thalassinoides* sometimes contain scratch marks, droppings or the bodily remains of the crustaceans which made them.
- *Teichichnus* has a distinctive form produced by the stacking of thin 'tongues' of sediment, atop one another. They are again believed to be fodinichnia, with the organism adopting the habit of retracing the same route through varying heights of the sediment, which would allow it to avoid going over the same area. These 'tongues' are often quite sinuous, reflecting perhaps a more nutrient-poor environment in which the feeding animals had to cover a greater area of sediment, in order to acquire sufficient nourishment.
- *Trypanites* are elongated cylindrical borings in calcareous substrates such as shells, carbonate hardgrounds and limestones. Usually produced by worms of various types and sipunculids.

Other notable trace fossils

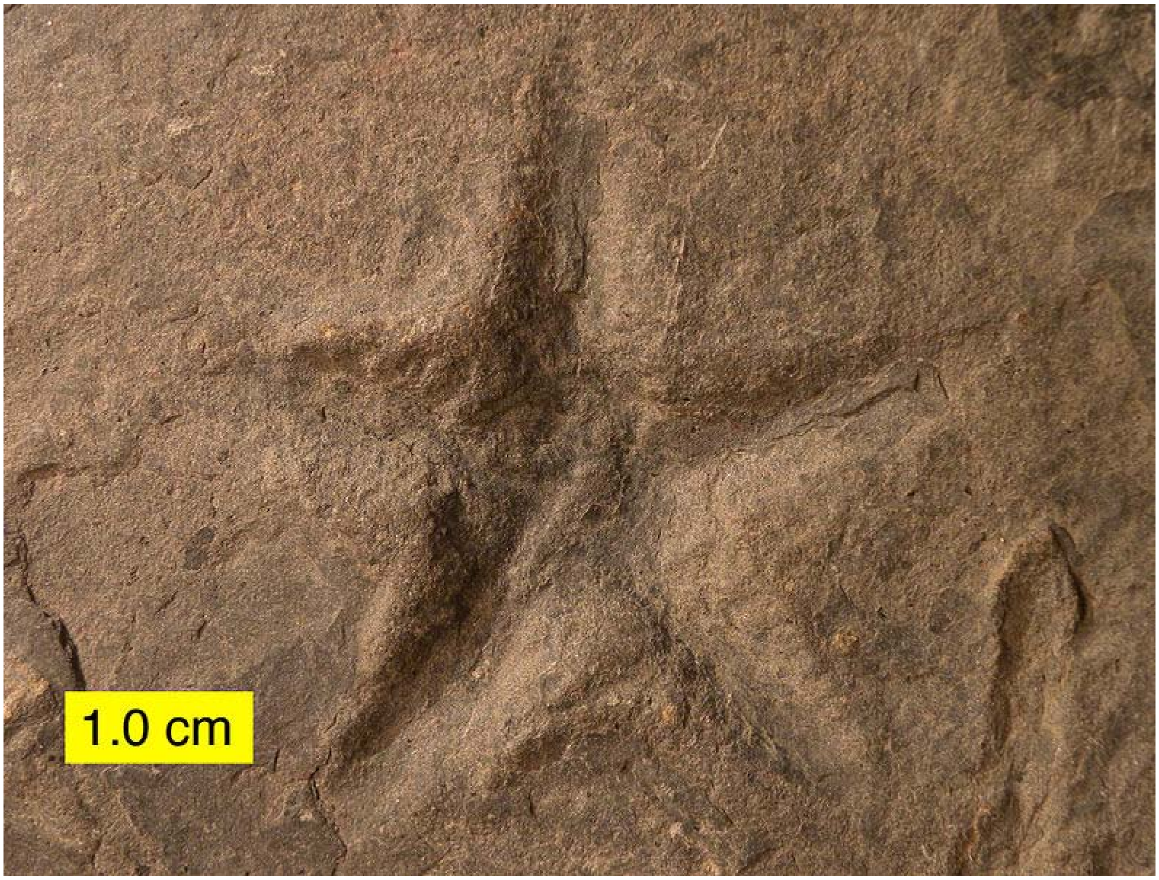
Less ambiguous than the above ichnogenera, are the traces left behind by invertebrates such as *Hibbertopterus*, a giant "sea scorpion" or eurypterid of the early Paleozoic era. This marine arthropod produced a spectacular hibbertopteroid track preserved in Scotland.

Bioerosion through time has produced a magnificent record of borings, gnawings, scratchings and scrapings on hard substrates. These trace fossils are usually divided into macroborings and microborings. Bioerosion intensity and diversity is punctuated by two events. One is called the Ordovician Bioerosion Revolution and the other was in the Jurassic.

The oldest types of tetrapod tail-and-foot prints date back to the latter Devonian period. These vertebrate impressions have been found in Ireland, Scotland, Pennsylvania, and Australia.

Important human trace fossils are the Laetoli (Tanzania) footprints, imprinted in volcanic ash 3.7 Ma (million years ago) -- probably by an early Australopithecus.

Confusion with other types of fossils



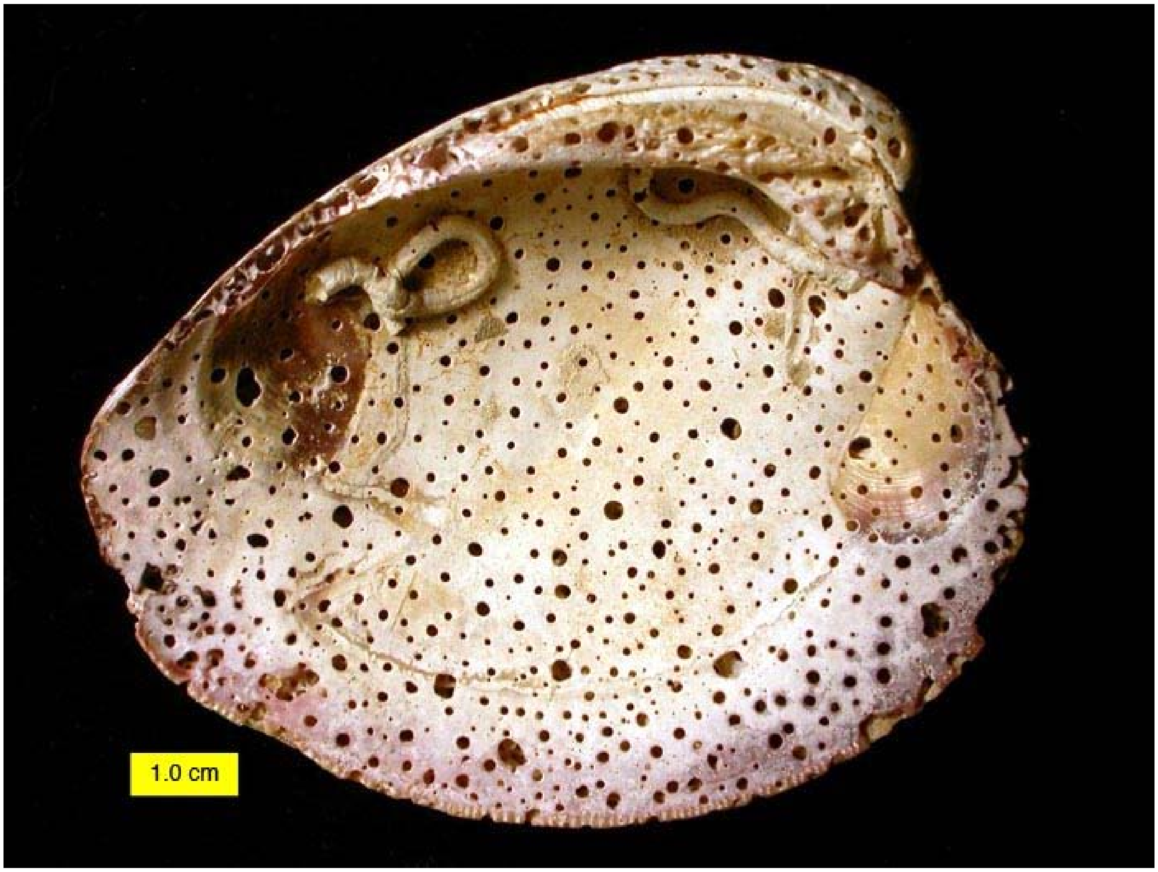
Asteriacites (sea star trace fossil) from the Devonian of northeastern Ohio. It appears at first to be an external mold of the body, but the sediment piled between the rays shows that it is a burrow.

Trace fossils are not body casts. The Ediacara biota, for instance, primarily comprises the casts of organisms in sediment. Similarly, a footprint is not a simple replica of the sole of the foot, and the resting trace of a seastar has different details than an impression of a seastar.

Early paleobotanists misidentified a wide variety of structures they found on the bedding planes of sedimentary rocks as fucoids (Fucales, a kind of brown algae or seaweed). However, even during the earliest decades of the study of ichnology, some fossils were recognized as animal footprints and burrows. Studies in the 1880s by A. G. Nathorst and Joseph F. James comparing 'fucoids' to modern traces made it increasingly clear that most of the specimens identified as fossil fucoids were animal trails and burrows. True fossil fucoids are quite rare.

Pseudofossils, which are *not* true fossils, should also not be confused with ichnofossils, which are true indications of prehistoric life.

Numerous borings in a Cretaceous cobble, Faringdon, England.



Sponge borings (*Entobia*) and encrusters on a modern bivalve shell, North Carolina.

Helminthopsis ichnosp.; a trace fossil from the Logan Formation (Lower Carboniferous) of Wooster, Ohio.

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

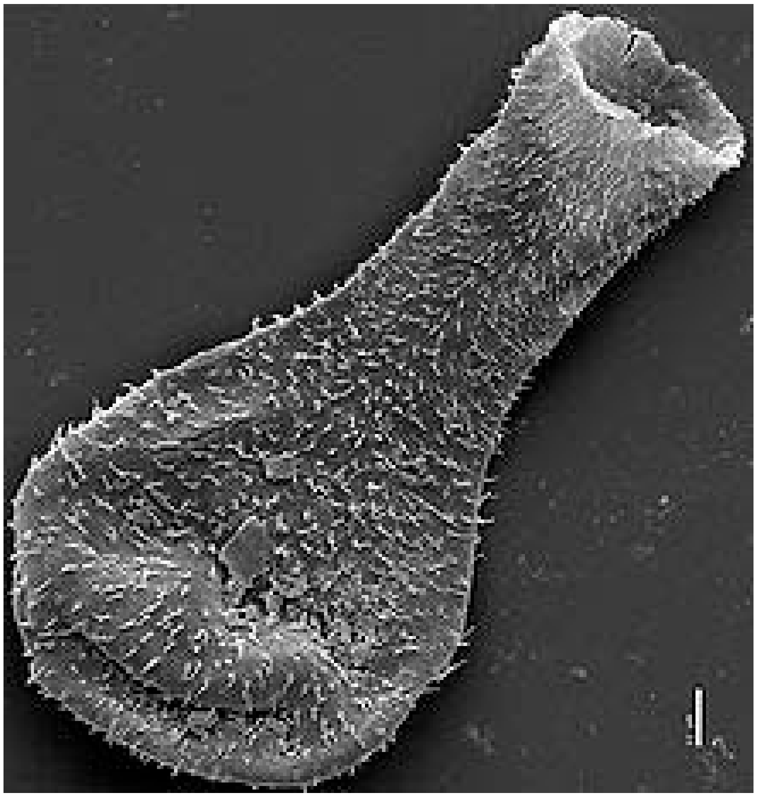
Chapter 7

Chitinozoan

Chitinozoan

Temporal range: 489–358 Ma

Tremadoc (lowest Ordovician) - Kinderhookian (lowest Carboniferous)



Scanning electron micrograph of a late Silurian chitinozoan from the Burgsvik beds showing flask shape

Scientific classification

Kingdom:	Animalia
Phylum:	*incertae sedis*

Class:	**Chitinozoa** Eisenack 1931
Order:	Operculatifera Prosomatifera Eisenack 1972

Groups

- Conochitinidae
- Desmochitinidae
- Lagenochitinidae

Chitinozoa (singular: chitinozoan, plural: chitinozoans) are a taxon of flask-shaped, organic walled marine microfossils produced by an as yet unknown animal. Common from the Ordovician to Devonian periods (i.e. the mid-Paleozoic), the millimetre-scale organisms are abundant in almost all types of marine sediment across the globe. This wide distribution, and their rapid pace of evolution, makes them valuable biostratigraphic markers.

Their bizarre form has made classification and ecological reconstruction difficult. Since their discovery in 1931, suggestions of protist, plant, and fungal affinities have all been entertained. The organisms have been better understood as improvements in microscopy facilitated the study of their fine structure, and there is mounting evidence to suggest that they represent either the eggs or juvenile stage of a marine animal.

The ecology of chitinozoa is also open to speculation; some may have floated in the water column, where others may have attached themselves to other organisms. Most species were particular about their living conditions, and tend to be most common in specific paleoenvironments. Their abundance also varied with the seasons.

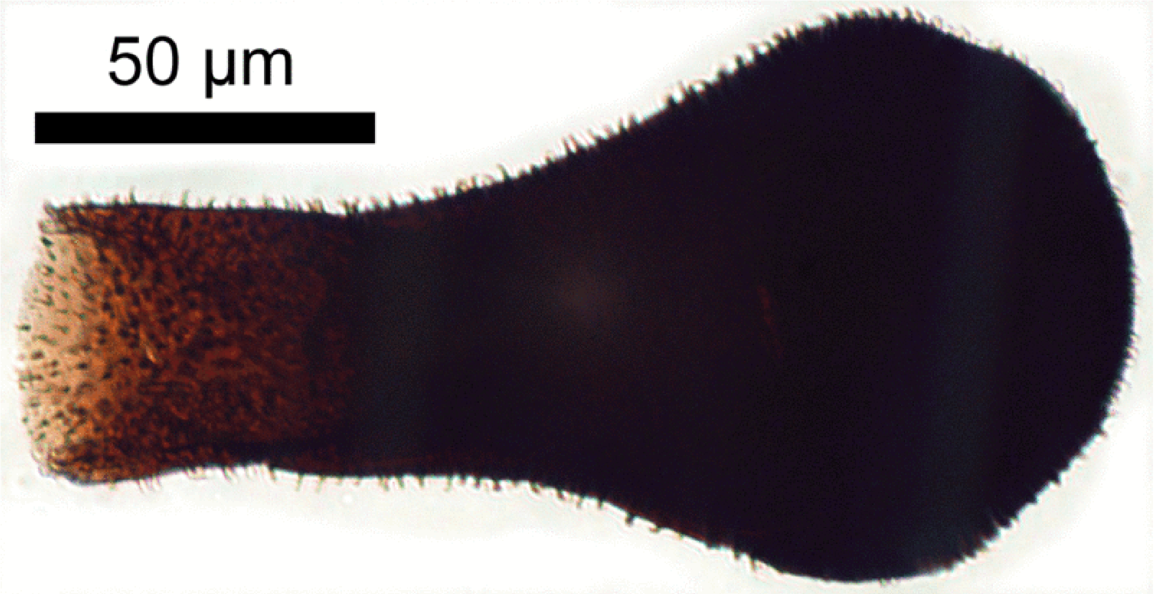
Appearance

Chitinozoa range in length from around 50 to 2000 micrometres. They appear dark to almost opaque when viewed under an optical microscope. External ornamentation is often preserved on the surface of the fossils, in the form of hairs, loops or protrusions, which are sometimes as large as the chamber itself. The range and complexity of ornament increased with time, against a backdrop of decreasing organism size. The earliest Ordovician species were large and smooth-walled; by the mid-Ordovician a large and expanding variety of ornament, and of hollow appendages, was evident. While shorter appendages are generally solid, larger protrusions tend to be hollow, with some of the largest displaying a spongy internal structure. However, even hollow appendages leave no mark on the inner wall of the organisms: this may suggest that they were secreted or attached from the outside. There is some debate about the number of layers present in the organisms' walls: up to three layers have been reported, with the internal wall often ornamented; some specimens only appear to display one. The multitude of walls may indeed reflect the construction of the organism, but could be a result of the preservational process.

"Immature" or juvenile examples of Chitinozoans have not been found; this may suggest that they didn't "grow", that they were moults (unlikely), or that the fossilisable parts of the organism only formed after the developmental process was complete.

Most chitinozoans are found as isolated fossils, but chains of multiple tests, joined from aperture to base, have been reported from all genera. Very long chains tend to take the form of a spring. Occasionally, clusters or condensed chains are found, packed in an organic "cocoon".

Classification



Scanning electron microscope images, such as that in the taxobox, are far more illuminating than those taken in **transmitted light**.

Alfred Eisenack's original description of the Chitinozoans placed them in three families, spanning seven genera, based on morphological grounds. Further genera were identified, at first on an annual basis, as time progressed. Since its publication in 1931, Eisenack's original classification has been much honed by these additional discoveries, as well as advances in microscopy. The advent of the scanning electron microscope in the 1970s allowed the improved detection of surface ornamentation which is hugely important in identification - as can be appreciated by a comparison of the images on this page. Even the light microscope image here is of far greater quality than could have been achieved earlier in the century, using poorly preserved specimens and less advanced microscopes. The original three families proposed by Eisenack represented the best classification possible with available data, based largely on the presence or absence of chains of organisms and the chamber's shape. The orders were subsequently revised to conform better to Linnean taxonomy, placing related organisms more closely together. This was made possible as scientific advances permitted the identification of distinctive traits in organisms across Eisenack's groups. Features of the base and neck, the presence of spines, and perforations or connections are now considered the most useful diagnostic features.

Relationships

What were the Chitinozoans? This question has been asked since their discovery in 1930, and we are little closer to an answer today. In order to address the issue, a combination of ecological, taphonomical and practical factors have to be considered.

Amoebæ

Eisenack's original guess was that the Chitinozoa were of the rhizopod order Testacea, since similar chitin-based tests were produced by the extant members of this group. However, the chemistry of these tests differs from that of the fossils, and modern Testacea are almost exclusively fresh-water - an extremely different environment. Within a year, he had abandoned this initial idea.

Photosynthesisers

Arguments put forwards by Obut (1973) proposed that the organisms were one-celled "plants" similar to the dinoflagellates, which would now be grouped into the chromalveolata. However, as mentioned previously, spines and appendages are attached from the exterior of the vessel: only animals have the cellular machinery necessary to perform such a feat. Further, no analogy for the cocoon envelope can be found in this kingdom.

Young graptolites

Chitinozoa may have been immature **graptolites**.

The graptolites are colonial organic walled fossils which also occurred from the Ordovician to the Devonian; only part of their life cycle is known and it is not clear how they reproduced. It has been suggested that the Chitinozoa may represent the pre-sicula stages of graptolites - the period between the colony's sexual reproduction, and the formation of a new colony. This hypothesis appears to be supported by the co-occurrence of graptolite and chitinozoan fossils, whose abundances appear to mirror one another. The similar chemical composition of the fossils has been seized by both sides of the argument. Proponents suggest that the use of the same chemical framework is an indicator that the two may be related. However, this factor means that situations favouring the preservation of one will also tend to preserve the other - and the preparation techniques used to extract the fossils will also favour or disfavour the two groups equally. Therefore, the apparent co-occurrence of the two fossils may merely be an artifact of their similar composition. The hypothesis struggles to explain the continuing abundance of chitinozoans after the middle Devonian, when graptolites became increasingly rare.

Chitinozoa might represent **gastropod egg** sacs.

Eggs

The test of the Chitinozoa was fixed - there was no scope for any parts of it to move or rotate. This makes it seem likely that the tests were containers, to protect whatever was inside - whether that was a "hibernating" or encysted organism, or a clutch of hatching eggs. There are several arguments behind an association of the chitinozoans with annelids or gastropods, and it is not impossible that the chitinozoans are a convergent phenomenon laid by both groups. In fact, the spirally coiled nature of chitinozoan chains has been used to suggest that they were laid by a spirally coiled organism, such as the gastropods; were this inference true, uncoiled chains could be to be attributed to the (straight) annelid worms or other organisms.

Recent excavations of the Soom Shale, an Ordovician konservat-lagerstätten in South Africa, have yielded chitinozoans alongside a wide range of other organisms. It has been suggested that if whatever organism created the Chitinozoa was fossilisable, it would be present in the Soom biota — from which gastropods and graptolites are notable in their absence. Most organisms present in the shale can be ruled out for a variety of reasons, but polychaete worms, *Promissum* conodonts and orthocone cephalopods remain as likely candidates. However, further evidence connecting chitinozoans to any of these groups is circumstantial at best.

Ecology

It is not immediately clear what mode of life was occupied by these improbably shaped fossils, and an answer only becomes apparent after following several lines of reasoning.

The fossils' restriction to marine sediments can be taken as sound evidence that the organisms dwelt in the Palæozoic seas - which presents three main modes of life:

- Infaunal — living within the sediment - the "burrowers"
- Benthic — dwelling upon the sea floor, perhaps anchored in place - the "sitters"
- Pelagic — free-floating in the water column - the "drifters"

An infaunal mode of life can be quickly ruled out, as the fossils are sometimes found in alignment with the depositing current; as nothing attached them to the bottom, they must have fallen from the water column.

The ornament of the chitinozoans may cast light on the question. Whilst in some cases a defensive role - by making the vessel larger, and thus less digestible by would-be predators - seems probable, it is not impossible that the protrusions may have anchored the organisms to the sea floor. However, their low-density construction makes this unlikely: perhaps more plausible is that they acted to attach to other organisms. Longer spines also make the organisms more buoyant, by decreasing their Rayleigh number (i.e. increasing the relative importance of water's viscosity) — it is therefore possible that at least the long-spined chitinozoans were planktonic "floaters". On the other hand, the walls of some chitinozoans were probably too thick and dense to allow them to float.

Whilst little is known about their interactions with other organisms, small holes in the tests of some chitinozoans are evidence that they were hosts to some parasites. Although some forms have been reinterpreted as "pock-marks" caused by the disintegration of the diagenetic mineral pyrite, the clustering of cylindrical holes around the chamber — where the flesh of the organism was likely to be concentrated — is evidence for a biological cause.

Growth rings in **corals** can reach a daily resolution.

Corals in Gotland with daily growth markings have been found in association with abundant chitinozoans, which allow the detection of seasonal variation in chitinozoan abundance. A peak in abundance during the late autumn months is observed, with the maxima for different species occurring on different dates. Such a pattern is also observed in modern-day tropical zooplankton. The diversity of living habits is also reflected by the depth of water and distance from the shore. Different species are found in highest abundance at different depths. While deeper waters around 40 km from the shoreline are generally the optimal environment, some species appear to prefer very shallow water. On the whole, chitinozoans are less abundant in turbulent waters or reef environments, implying an aversion to such regimes when alive, if it is not an effect of sedimentary focusing. Chitinozoans also become rarer in shallower water - although the reverse is not necessarily true. They cannot survive freshwater input.

Stratigraphic application

Since Alfred Eisenack first recognised and named the group in 1930, the Chitinozoa have proven incredibly useful as a stratigraphic markers in biostratigraphy during the Ordovician, Silurian and Devonian periods. Their utility is due to the rapidity of their morphological evolution, their abundance — the most productive samples bearing almost a thousand tests per gram — and the easy identification (due largely to the large variation in shapes) and short lifetimes (<10 million years) of most species. They are also widely distributed and appear in a variety of marine depositional settings, making correlation easier; better still, they can often be recognised in even quite strongly metamorphosed rocks. However, convergence of morphological form to similar environments sometimes leads to the mistaken identification of a species in several areas separated by vast differences in space and time, but sharing a similar depositional environment; clearly, this can cause major problems if the organisms are interpreted as being the same species. Aside from the acritarchs, chitinozoans were the only reliable means of correlating palæozoic units until the late 1960s, when the detailed study of conodonts and graptolites fully unleashed their stratigraphic potential.

Chapter 8

Hallucigenia

Hallucigenia
Temporal range: Lower to Middle Cambrian

Artist's rendering of *Hallucigenia* according to the modern interpretation

A fossil of *Hallucigenia* from the Burgess shale

Scientific classification

Kingdom:	Animalia
Phylum:	?Onychophora
Class:	?Xenusia
Order:	?Scleronychophora

Family: **Hallucigeniidae**
Morris, 1977

Genus: ***Hallucigenia***
Morris, 1977

Species

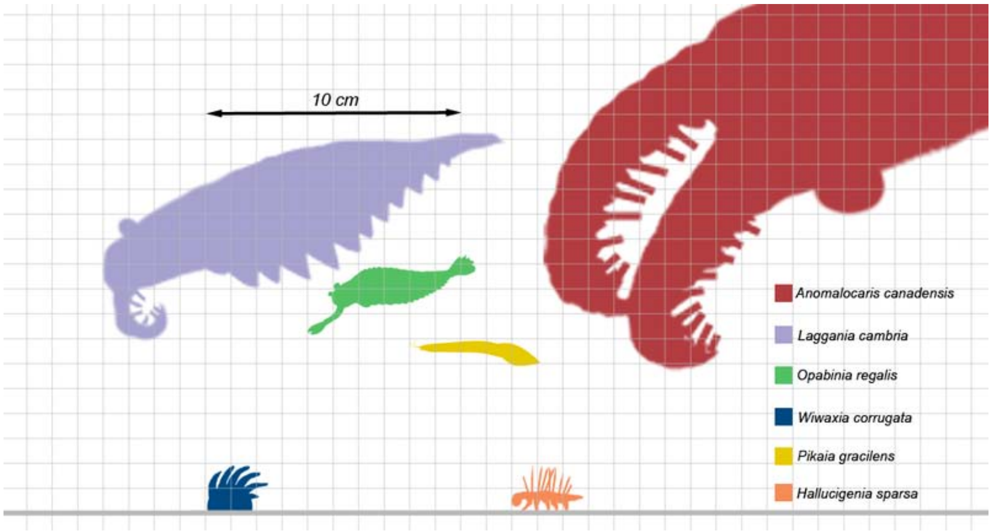
- *H. sparsa* Morris, 1977 (type)
- *H. fortis* Hou & Bergström, 1995

Synonyms

Canadia sparsa

Hallucigenia is an extinct genus of animal found as fossils in the Middle Cambrian-aged Burgess Shale formation of British Columbia, Canada, represented by the species *H. sparsa*, and in the Lower Cambrian Maotianshan shale of China, represented by the species *H. fortis*. The genus name was coined by Simon Conway Morris when he re-examined the various specimens of Charles Walcott's Burgess Shale worm genus *Canadia* in 1979. Conway Morris found that what Walcott had called one genus in fact included several quite different animals. One of them was so unusual that nothing about it made much sense. Since the species clearly was not a polychaete worm, Conway Morris had to provide a new generic name to replace *Canadia*. Conway Morris named the species *Hallucigenia sparsa* because of its "bizarre and dream-like quality" (like a hallucination). *Hallucigenia* was initially considered by Stephen Jay Gould to be unrelated to any living species, but most palaeontologists now believe that the species was a relative of modern arthropods.

Description and investigation

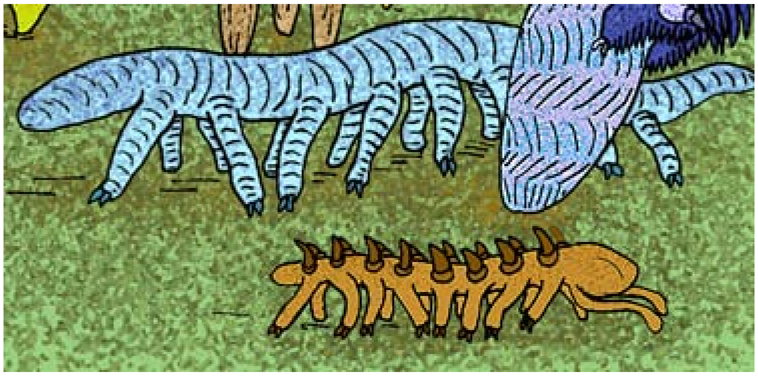


Scale diagram of various Burgess Shale invertebrates, *Hallucigenia sparsa* is small orange figure at bottom.

109 specimens of *Hallucigenia* are known from the Greater Phyllopod bed, where they comprise 0.3% of the community. The 0.5 to 3 cm-long animal is wormlike — that is, long and narrow — with a poorly defined blob, or stain, on one end. This "blob" was arbitrarily designated the 'head' even though it had none of the features generally associated with heads: mouth, eyes, or other sensory organs. According to Morris' original interpretation, the animal has seven pincer-tipped tentacles lined up on one side and seven pairs of jointed spines on the other. Six of the tentacles were paired with spines, with one in front of the spines. There were also six smaller tentacles which may be configured in three pairs behind the seven larger ones. In addition, the body continued with a flexible, tube-like, tail-like extension behind the tentacles.

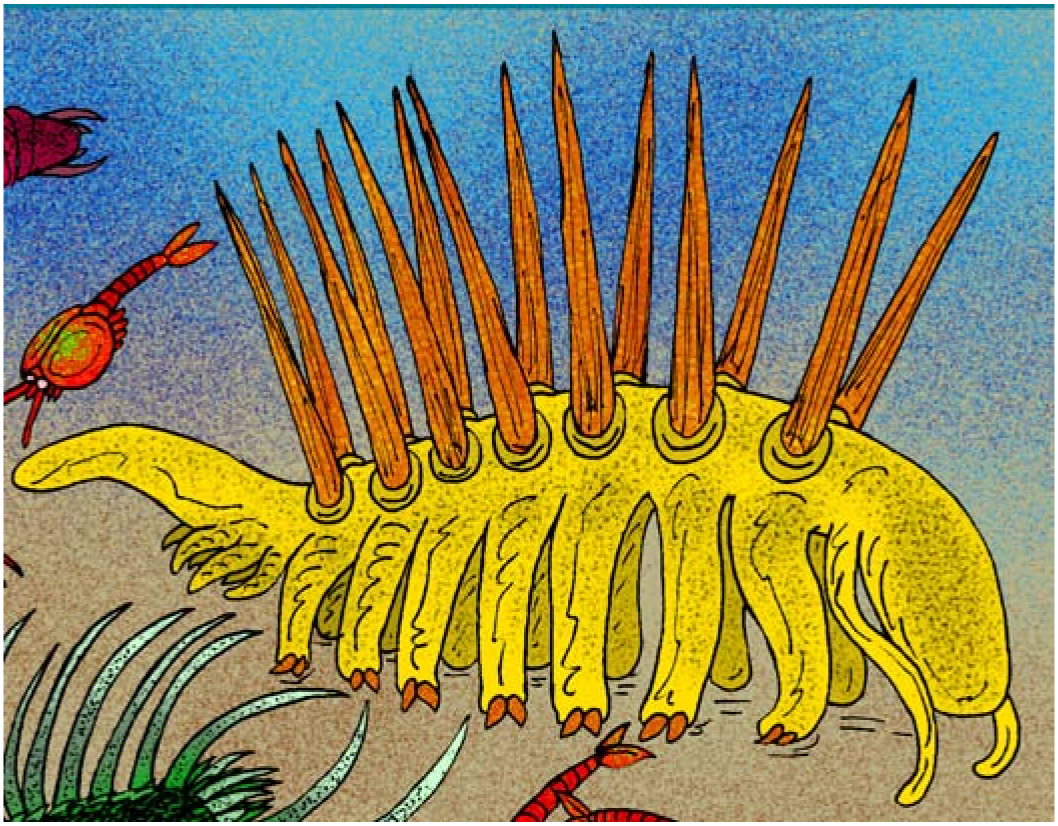
Faced with an animal that had no obvious head and two types of appendages, neither of which seemed appropriate for any reasonable form of locomotion, Morris assigned the blob as the head and hypothesized that the spines were legs and that the tentacles were feeding appendages. Morris was able to demonstrate a workable, if improbable, method of walking on the spines. Only the forward tentacles could easily reach to the 'head', meaning that a mouth on the head would have to be fed by passing food along the line of tentacles. Morris suggested that a hollow tube within each of the tentacles might be a *mouth*. This raised questions such as how it would walk on the stiff legs, but it was accepted as the best available interpretation. A picture of the animal as reconstructed by Morris can be found at Yvonne Navarro's website.

An alternative interpretation considered *Hallucigenia* to be an appendage of a larger, unknown animal. There had been precedent for this, as the species Anomalocaris had been originally identified as three separate creatures before being identified as a single huge (for its time) 3-foot-long (0.91 m) creature. Given the uncertainty of its taxonomy, *Hallucigenia* was tentatively placed within the phylum Lobopodia, a catch-all clade containing numerous odd "worms with legs."



Reconstruction of *H. fortis* as an onychophoran.

In 1991, Lars Ramskold and Hou Xianguang, working with additional specimens of a "hallucigenid," *Microdictyon*, from the lower Cambrian Maotianshan shales of China, reinterpreted *Hallucigenia* as an Onychophore. They inverted it, interpreting the tentacles, which they believe to be paired, as walking structures and the spines as protective. Interestingly, none of the 30 or so known Burgess Shale specimens shows any sign of pairing in the large tentacles; nor do their Chinese counterparts. The pairing is based on a dissection of the actual fossil, which revealed what is probably a second tentacle structure. Ramskold and Hou also believe that the blob-like 'head' is actually a stain that appears in many specimens, not a preserved portion of the anatomy.



Reconstruction of *H. sparsa* as an onychophoran.

Though Ramskold and Hou's is the accepted modern interpretation, it is far from problem-free. Unlike its contemporary *Aysheaia*, *Hallucigenia* has very little resemblance to modern Onychophora. The elongated, and clawed legs bear little resemblance to the paired annulated legs of the Onychophora. It is unknown what the spines were made of and how much 'protection' they offered. They do not seem to be preserved independent of the soft-shelled animals as carbonate or chitinous shells would probably be. It is not easy to explain why 30 or more specimens — each hypothesized to have seven pairs of rather long, flexible legs — do not show even one example of paired legs. But at least this reconstruction of the animal can plausibly walk, and the spines serve a reasonable purpose. A picture of this reconstruction as well as a photograph of an actual fossil can be seen on the Geological Survey of Canada's website.

Some paleontologists accept Ramskold and Hou's interpretation of the animal's legs, spines, and head, but also believe that *Hallucigenia* might be an "armored lobopod" related to *Anomalocaris*. This does not rule out this bizarre creature also being related to the Onychophora, but rather may point to it coming from some time during or near the split of the two closely related groups.

Fossil specimen on display at the Smithsonian in Washington, DC

In 2002, Desmond Collins suggested that new *Hallucigenia* fossils showed male and female forms, one with "a rigid trunk, robust neck and a globular head" and the other thinner, and with a small head.

Robotic application

FuRo robotics, a Japanese technology company, took inspiration from the Hallucigenia's unique anatomy in designing their Hallucigenia-I and Halluc-II concept vehicles. Working prototypes of these vehicles, which have 8 wheels on the end of 8 robotic appendages, can move in any direction and can climb over uneven terrain.

Chapter 9

Kimberella

Kimberella
Temporal range: Ediacaran 558–555 Ma

Fossil of *Kimberella quadrata*.

Cast of a partial *Kimberella* fossil.

Scientific classification

Kingdom:	Animalia
Subkingdom:	Eumetazoa
(unranked):	Bilateria

Phylum:	Mollusca?
Genus:	***Kimberella*** Wade, 1972
Species:	***K. quadrata*** Glaessner & Wade, 1966

Synonyms

Kimberia quadrata Glaessner & Wade, 1966

Kimberella is a monospecific genus of bilaterian known only from rocks of the Ediacaran period. The slug-like organism fed by scratching the microbial surface on which it dwelt in a manner similar to the molluscs, although its affinity with this group is contentious.

Specimens were first found in Australia's Ediacara Hills, but recent research has concentrated on the numerous finds near the White Sea in Russia, which cover an interval of time from 555 to 558 million years ago. As with many fossils from this time, its evolutionary relationships to other organisms is hotly debated. Paleontologists initially classified *Kimberella* as a type of jellyfish, but since 1997 features of its anatomy and its association with scratch marks resembling those made by a radula have been interpreted as signs that it may have been a mollusc. Although some paleontologists dispute its classification as a mollusc, it is generally accepted as being at least a bilaterian.

The classification of *Kimberella* is important for scientific understanding of the Cambrian explosion: if it was a mollusc or at least a protostome, the protostome and deuterostome lineages must have diverged significantly before 555 million years ago. Even if it was a bilaterian but not a mollusc, its age would indicate that animals were diversifying well before the start of the Cambrian.

Etymology

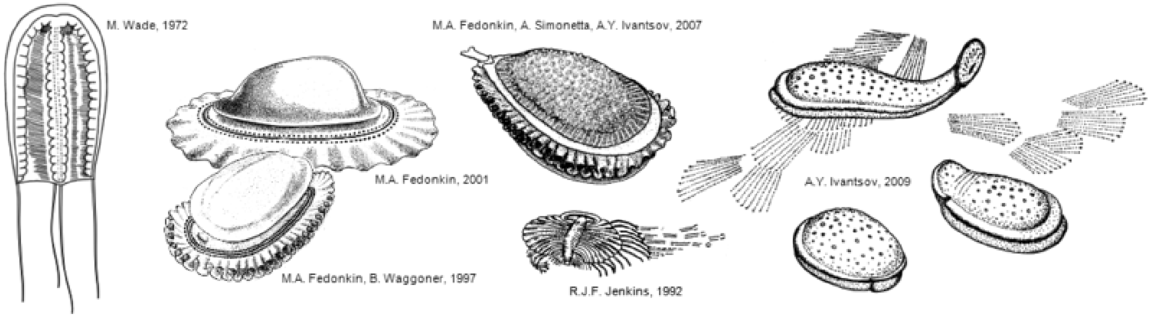
Restoration

The genus is named after Mr. John Kimber, student, teacher, and collector who lost his life during an expedition to Central Australia in 1964. Originally it was described with the name *Kimberia*. Dr. N. H. Ludbrook drew attention to the fact that the name *Kimberia* is preoccupied by *Kimberia* Cotton and Woods, a turtle subgenus. Accordingly the new name *Kimberella* was proposed by Mary Wade in 1972.

Occurrence

Kimberella has been found both in the Ediacara Hills of South Australia and in the Ust' Pinega Formation in the White Sea region of Russia. The White Sea fossils are often associated with the Ediacaran "animals" *Tribrachidium* and *Dickinsonia*; meandering trace fossil trails, possibly made by *Kimberella* itself; and algae. Beds in the White Sea succession have been dated to 555.3 ± 0.3 million years ago and 558 million years ago by radiometric dating, using uranium-lead ratios in zircons found in volcanic ash layers that are sandwiched between layers that contain *Kimberella* fossils. *Kimberella* fossils are also known from beds older and younger than this precisely dated range. The fossils from the Ediacara Hills have not been dated precisely.

Description



History of *Kimberella quadrata* reconstruction:
* M. Wade, 1972 – Cubozoa.
* M.A. Fedonkin, B. Waggoner, 1997, M.A. Fedonkin, 2001 – mollusc-like organism with soft shell and big foot.
* M.A. Fedonkin, A. Simonetta, A.Y. Ivantsov, 2007 – mollusc-like organism with soft shell and proboscis carrying two hook-like teeth at its end.
* R. J. F. Jenkins, 1992 – hypothetical trilobite-like arthropod as a maker of feeding traces of *Kimberella*
* A.Y. Ivantsov, 2009 – no complete consolidated shell, but with mineral sclerites and several teeth in its mouth.

Over 1000 specimens, representing organisms of all stages of maturity, have now been found in the White Sea area at the bottom of fine-grained sandstone layers. The large number of specimens, the small grain-size of the sediments and the variety of circumstances in which specimens were preserved provide detailed information about *Kimberella*'s external form, internal anatomy, locomotion and feeding style.

All of the fossils are oval in outline. Elongated specimens illustrate that the organism was capable of stretching in an anterior-posterior direction, perhaps by as much as a factor of two. The only type of symmetry visible in the White Sea specimens is bilateral; there is no sign of any of the kinds of radial symmetry that are normal in the Cnidaria, the group that includes jellyfish, sea anemones and hydras. The Australian fossils were originally described as a type of jellyfish, but this is inconsistent with the bilateral symmetry in the fossils. The White Sea fossils and the surrounding sediments also show that *Kimberella* lived on the surface of the sea-floor.

Kimberella had a dorsal integument that has been described as a non-mineralized "shell"; in the larger specimens this reached up to 15 cm in length, 5 to 7 cm in width, and was 3 to 4 cm high; the smallest specimens are only about 2–3 mm long. The shell was stiff but flexible, and appears to have been non-mineralized, becoming tougher as it grew larger (and presumably thicker) in more mature specimens. The deformation observed in elongated and folded specimens illustrates that the shell was highly malleable; perhaps, rather than a single integument, it consisted of an aggregation of (mineralized?) sclerites. At its highest point was a hood-like structure, forming what is thought to be the front. In some specimens, the inner surface of the shell bears stripes spanning the width of the creature; these may represent the attachment sites of muscles. Similar stripes around the edge of the shell may have been connected to muscles involved in retracting the muscular foot into the shell.

The long axis of the organism is marked by a raised ridge; the middle axis is slightly humped. Kimberella′s body had no visible segmentation but had a series of repeated "modules". Each module included a well-developed band of dorso-ventral muscles running from the top to the single, broad, muscular "foot", and smaller transverse ventral muscles from side to side on the underside of the body. The combination of the bands of dorso-ventral and transverse ventral muscles enabled Kimberella to move by making the foot ripple.

The body also had a frilled fringe that may have been part of the animal's respiratory system, performing a function similar to that of gills. The fact that the fringe extended well beyond the shell may indicate that *Kimberella*′s "gills" were inefficient and needed a large area, or that there were no effective predators on *Kimberella* and the shell's main function was to provide a platform for the muscles.

Ecology

Kimberella dwelt in shallow waters (up to tens of meters in depth), sharing the calm, well-oxygenated sea floor with photosynthetic organisms and microbial mats. Assemblages bearing *Kimberella* often also bear fossils of *Yorgia*, *Dickinsonia*, *Tribrachidium* and *Charniodiscus*, suggesting that it lived alongside these organisms.

Kimberella probably grazed on microbial mats, but a selective predatory habit cannot be ruled out. As it ate, it moved "backwards"; the trail thus created was destroyed by the subsequent grazing activity. Fans of grooves are often found radiating from the "head" end of the organism; these indicate that the organism stayed in one place, and raked the surface of the microbial mat towards it by extension of its head, which bore a number of regularly spaced "teeth".

The lack of evidence to the contrary suggests that the organisms reproduced sexually.

The waters in which *Kimberella* dwelt were occasionally disturbed by sandy currents, caused when sediments were whipped up by storms or meltwater discharge, and washed over the creatures. In response to this stress, the organisms appear to have retracted their soft parts into their shells; apparently they could not move fast enough to outrun the currents. Some organisms survived the current, and attempted to burrow out of the sand that had been deposited above them; some unsuccessful attempts can be seen where juveniles were fossilised at the end of a burrow a few centimetres long.

Preservation

Kimberella fossils are generally preserved on top of a clay-rich bed and beneath a sandy bed. All fossils are preserved as depressions in the bases of beds, implying that the organism, although not mineralised, was firm enough to resist being crushed as sediment accumulated above it; as the soft parts of the organism decayed, the soft muds underneath would be squeezed up into the shell, preserving the shape of the organism.

Preservation of most specimens was made possible by the fast sedimentation that quickly cut the organism off from seawater; it may also have been enhanced by the decay products of the rotting organism, which could have helped the overlying sediment to mineralise and harden. It has been suggested that a mucus trail produced by the organism may have assisted its preservation, but experiments suggest that mucus disintegrates too easily to play a role in binding sediment together.

Classification

Feeding trace of *Kimberella*

All the *Kimberella* fossils found so far are assigned to one species, *K. quadrata*. The first specimens were discovered in Australia in 1959. They were originally classified as jellyfish by Martin Glaessner and Mary Wade in 1966, and then as box jellyfish by Wade in 1972, a view that remained popular until the fossils of the White sea region were discovered; these prompted a reinterpretation. Research on these specimens by Mikhail A. Fedonkin, initially with Benjamin M. Waggoner in 1997, led to *Kimberella* being recognised as the oldest well-documented triploblastic bilaterian organism — not a jellyfish at all.

So far *Kimberella* fossils show no sign of a radula, the toothed chitinous "tongue" that is the diagnostic feature of modern molluscs, excluding bivalves. Since radulae are very rarely preserved in fossil molluscs, its absence does not necessarily mean that *K. quadrata* did not have one. The rocks in the immediate vicinity of *Kimberella* fossils bear scratch marks that are very similar those made by the radulae of molluscs as they graze on microbial mats. These traces, named *Radulichnus*, have been interpreted as circumstantial evidence for the presence of a radula. In conjunction with the univalve shell, this has been taken to indicate *Kimberella* was a mollusc or very closely related to molluscs. In 2001 and 2007 Fedonkin suggested that the feeding mechanism might be a retractable proboscis with hook-like organs at its end. The feeding apparatus appears to differ in important respects to the radula, demonstrating that *Kimberella* is at best a stem-group mollusc.

However, sceptics feel that the available evidence is not enough to reliably identify *Kimberella* as a mollusc or near-mollusc, considering it presumptuous to call it anything more than a "possible" mollusc, or even just a "probable bilaterian". Nicholas J. Butterfield argues that *Kimberella's* association with *Radulichnus* marks is not strong evidence that it was a mollusc, as other groups of organisms bear structures capable of making similar marks. Indeed it has been argued that the shape of the feeding traces is incompatible with a radula, and that despite the molluscan body form, the lack of this synapomorphy places it well outside the molluscan crown group.

Theoretical importance

The Cambrian explosion is an apparently rapid increase in the variety of basic body structures of animals in the Early Cambrian period, starting after 543 million years ago and finishing before 518 million years ago. A few of the Early Cambrian fossils were already known in the mid-19th century, and Charles Darwin saw the apparently sudden appearance and diversification of animals as one of the main objections that could be made against his theory of evolution by natural selection.

The majority of animals more complex than jellyfish and other Cnidarians are split into two groups, the protostomes and deuterostomes. The mollusc-like features of *Kimberella* strongly suggest that it was a member of the protostomes. If so, this means that the protostome and deuterostome lineages must have split some time before *Kimberella* appeared — at least 558 million years ago, and hence well before the start of the Cambrian 542 million years ago. Even if it is not a protostome, it is widely accepted as a member of the more inclusive bilaterian clade. Since fossils of rather modern-looking Cnidarians have been found in the Doushantuo lagerstätte, the Cnidarian and bilaterian lineages would have diverged well over 580 million years ago.

Chapter 10

Wiwaxia

Wiwaxia **Temporal range: Upper Lower Cambrian–Mid Middle Cambrian**	

Fossil specimen on display at the Smithsonian in Washington, DC

Scientific classification [e]	
Kingdom:	Animalia
Superphylum:	Lophotrochozoa
Phylum:	*incertae sedis*
(unranked):	†Halwaxiida
Family:	†**Wiwaxiidae** Walcott, 1911
Genus:	†***Wiwaxia*** Walcott, 1911

Type species

Wiwaxia corrugata
(Matthew, 1899)

Species

W. corrugata (Matthew, 1899)
W. taijiangensis Zhao, Qian & Lee,

1994

Wiwaxia is a genus of soft-bodied, scale-covered animals known from Burgess shale type Lagerstätte dating from the upper Lower Cambrian to Middle Cambrian. The organisms are mainly known from dispersed sclerites; articulated specimens, where found, range from 3.4 millimetres (0.13 in) to a little over 5 centimetres (2.0 in) in length. The precise taxonomic affinities of the genus are a matter of ongoing debate amongst palaeontologists.

History of discovery

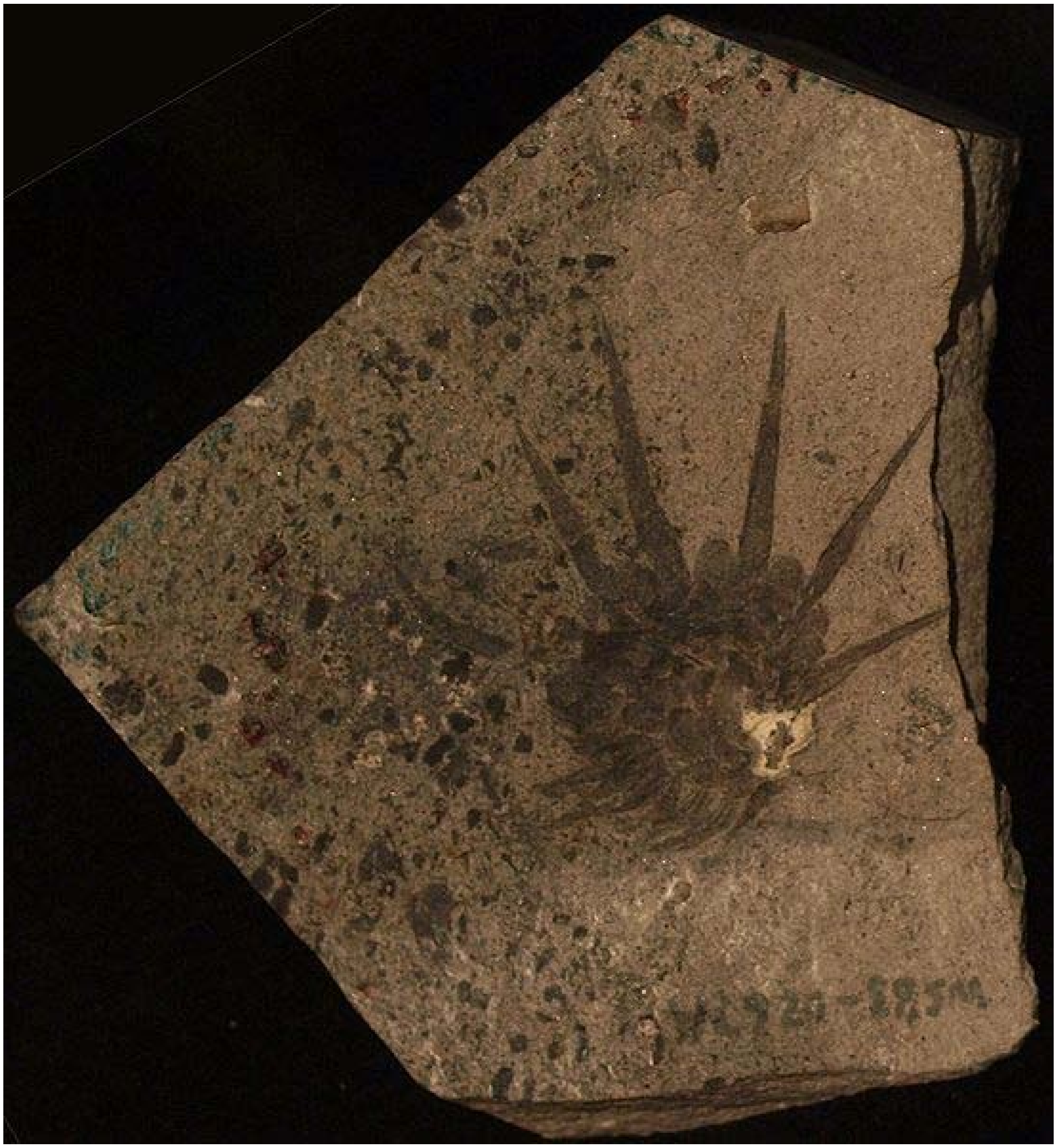
Fossil specimen in talus below the Walcott Quarry, with large body sclerites clearly visible, and longer spines oriented to the north-east of the image.

Wiwaxia was originally described by W.D. Matthew in 1899, from an isolated spine that had been found earlier in the Ogyopsis Shale, and classified as a hyolithid. Further specimens were found by American paleontologist Charles Doolittle Walcott in 1911 as a result of one of his field trips to the nearby Burgess Shale in the Canadian Rocky Mountains, and he classified it as a member of the polychaete group of annelid worms.

In 1966 and 1967 a team led by Harry B. Whittington revisited the Burgess Shale and found so many fossils that it took years to analyze them all, and *Wiwaxia* was one of the most difficult to analyze. 464 complete specimens of *Wiwaxia* are known from the

Greater Phyllopod bed, where they comprise 0.88% of the community. Eventually in 1985 Simon Conway Morris, then a member of Whittington's team, published a detailed description that concluded *Wiwaxia* was not a polychaete. All the known specimens came from in and around the Burgess Shale until 1991, when fragmentary fossils were reported from Australia's Georgina Basin. In 2004 additional finds which may represent two different species were reported from the same area.

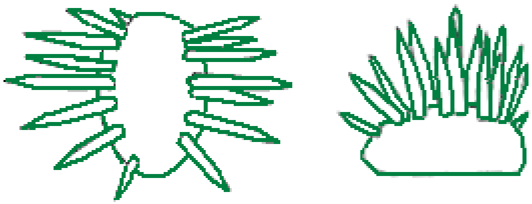
Occurrence



Parallel-oblique specimen of *W. corrugata* with widely-splayed spines.

Reasonably complete specimens have been found in the Burgess Shale, middle part of the Middle Cambrian with date 505 million years ago., and fragmentary specimens in nearby strata slightly older than and younger than the Burgess Shale, in China's lowermost Middle Cambrian beds of the Kaili Formation, in the Middle Cambrian beds of the Tyrovice Member, Buchava Formation of the Czech Republic, in the Lower Cambrian Mount Cap formation (Mackenzie Mountains, Canada), in the Emu Bay Shale of Kangaroo Island, South Australia, upper Botomian Stage of the Lower Cambrian, and in the Middle Botomian Sinsk Biota of the Siberia, Russia. These finds show that *Wiwaxia* and most of the other Burgess Shale type fauna were very widespread. The Chinese material is considered to represent a separate species; like *W. corrugata*, it possessed spines and regions of sclerites (although it is only known from disarticulated remains), but the sclerites bear a higher density of ribs, and there are two distinct thicknesses of rib (i.e. larger and smaller). Isolates spines are more common than sclerites in localities with a poor preservation potential, suggesting that the spines were more recalcitrant; however, in well-preserved sites such as the Phyllopod bed, spine and sclerite abundance is coparable in disarticulated instances to the proportions on complete fossils.

Description

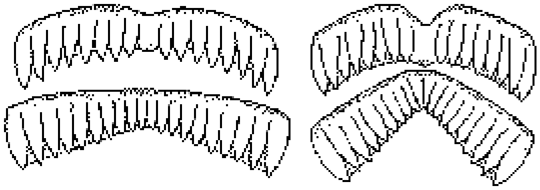


Wiwaxia viewed from top (moving up) and right

This concentrates on the species *Wiwaxia corrugata*, found in the Burgess Shale, since the other specimens consist only of fragments, while the Burgess Shale has provided at least 138 complete ones.

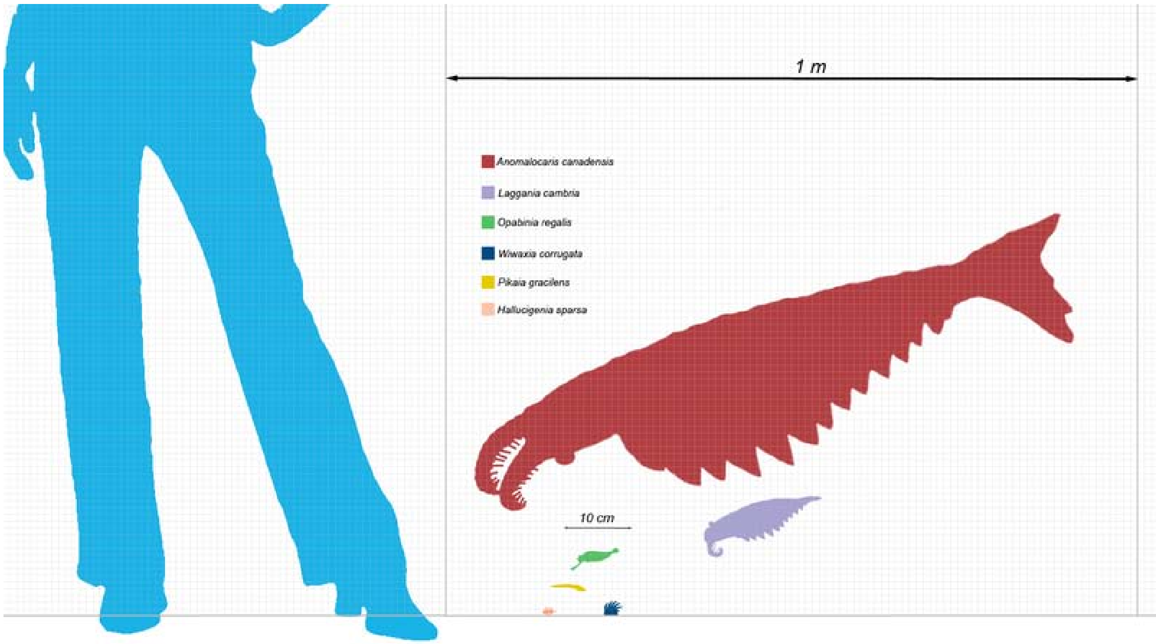
Wiwaxia was a bilaterally symmetrical animal. Viewed from the top the body was elliptical with no distinct head or tail, and from the front or rear it was almost rectangular. The most complete fossils fall into two size ranges: 2 centimetres (0.79 in) to 5 centimetres (2.0 in) long, which are thought to be adults; and 3.4 millimetres (0.13 in) to 1.5 centimetres (0.59 in), which are thought to be juveniles. Estimating their height is difficult because specimens were compressed after death; a specimen of the average length, 3.4 centimetres (1.3 in), may have been 1 centimetre (0.39 in) high excluding the spines on their backs. The ratio of width to length does not appear to change as the animals grew. The animal was covered in small ribbed armor plates called sclerites, that lay flat against the body, overlapped so that the rear of one covered the front of the one behind, and formed five main regions — the top, with 8-9 rows of sclerites; the upper part of the sides, with 11-12; the lower part of the sides, with 8; the front; and the area nearest the sea-floor, with 12-17 rows. Most of the sclerites were shaped like oval leaves, but the ventro-lateral ones, nearest the sea-floor, were crescent-shaped, rather like flattened bananas, and formed a single row with the tips pointing down. In addition there were two rows of ribbed spines running from to rear, one along each side of the top surface, and projecting out and slightly upwards, with a slight upwards curve near the tips. Specimens ranging from 11 millimetres (0.43 in) 52 millimetres (2.0 in) have about the same number of ventro-lateral sclerites just above the foot. On the other hand the number of spines seems to depend on the size of the specimen, up to about 12 per side. The number and spacing of the spines is asymmetrical in the specimens found, and this may have been natural rather than a result of events in the animal's life or after death. Although the spines in the middle of each row are usually the longest, up to 5 centimetres (2.0 in), a few specimens have rather short middle spines, perhaps because these were part-grown replacements. The smallest specimens may have lacked the long dorsal spines, which appear to have grown quickly in larger juveniles and then more slowly in adults.

Each sclerite was rooted separately in the body; the roots of body sclerites are 40% of the external length or a little less, while the roots of the spines are a little over 25% of the external length; all were rooted in pockets in the skin, rather like the follicles of mammalian hair. The roots of the body sclerites were significantly narrower than the sclerites, but the spines had roots about as wide as their bases; both types of root were made of fairly soft tissue. They bore protrusive, presumably structural, ribs on their upper and (seemingly) lower surfaces. The sclerites and spines were not mineralized, and the frayed appearance of some broken ones suggests a fibrous structure. They way they were preserved suggests they were not made of chitin, from which insects' exoskeletons are formed. They may have been made of tanned proteins or of collagen, which is the main component of cartilages and tendons in humans. Since the body sclerites had bases that were narrower than the hard external parts, it is hard to see how they grew. They may have enclosed soft tissue that could have secreted the hard walls, but there is no convincing evidence for this. Butterfield (1990) examined some sclerites under both optical and scanning electron microscopes and concluded that they were not hollow, and that the bases split and spread to form the blades, a pattern that is also seen in monocot leaves.



Wiwaxia usually had two tooth-rows: opened for feeding (left); folded (right). In both cases the front of the animal is at the top.

Wiwaxia's flat underside was soft and unarmored. Little is known of the internal anatomy, although the gut apparently ran straight and all the way from the front to the rear. At the front end of the gut, about 5 millimetres (0.20 in) from the animal's front in an average specimen about 2.5 centimetres (0.98 in) long, there was a feeding apparatus that consisted of two (or in rare large specimens three) rows of backward-pointing conical teeth. The feeding apparatus was tough enough to be frequently preserved, but unmineralized and fairly flexible, as it folded and retracted when not in use. It would have had to be pushed forward out of the mouth in order to feed. Even the smallest specimens have this type of apparatus, with two rows containing the same number of teeth as in larger ones. This indicates that *Wiwaxia*'s feeding habits remained the same throughout its life after the larval stage. The feeding apparatus may have acted as a rasp to scrape bacteria off the top of the microbial mat that covered the sea-floor, or as a rake to gather food particles that lay on the sea-floor.



Scale diagram of various Burgess Shale invertebrates, *Wiwaxia corrugata* in dark blue

Since there is no sign of eyes or tentacles, *Wiwaxia* may have relied mainly on chemical senses such as smell and taste. Its respiratory system is also unknown.

The long dorsal spines may have been a defense against predators, and finds of broken spines suggest that *Wiwaxia* was attacked. The animal appears to have crawled on the surface of the sea-floor feeding on particles that fell from higher levels of the sea. *Wiwaxia* shows no signs of legs and was probably too large to move on cilia, so it probably moved by muscular contraction that made its foot ripple. Juveniles may have burrowed into the sea-floor. In one specimen a small brachiopod, *Diraphora bellicostata*, appears to be attached to one of the ventro-lateral sclerites. This suggests that adult *Wiwaxia* did not burrow or even plough much into the sea-floor as they moved. Two other specimens of *Diraphora bellicostata* have been found attached to dorsal sclerites. *Wiwaxia* appears to have been solitary rather than gregarious.

Ontogeny

Wiwaxia grew by expansion rather than addition; that is to say it appears to have maintained a constant complement of scales as it grew, with each sclerite growing larger (by an unspecified means, probably by molting and replacement) and changing slightly in shape, but no new sclerites being inserted. 16–18 ventro-lateral sclerites are present on each side of a specimen, and the dorsal sclerites are arranged in 7–9 rows; the variation in number may be genuine but could reflect partial preservation. Its length:width ratio was constant through growth (although spineless "juveniles" may have been slightly flatter).

One juvenile specimen appears to be preserved while molting and not yet completely detached from its discarded armor. Its new set of spines seem less rigid than the old ones and slightly underdeveloped, as if the next stages were going to be inflated by body fluids and then hardening. The new armor may have had an internal volume 50% to 70% larger than the old one. Molting appears to have occurred all at once, as adult specimens shows no signs of interruptions in the sclerite armor that would indicate molting of parts of the armor or of individual sclerites. Since the bases of the body sclerites are relatively narrow and these is no sign of sclerites splitting during molting, withdrawing soft tissue from the old sclerites would probably have required the tissues to be broken down in to a more fluid form, as happens in the claws of lobsters and crabs when they molt. The skin must also have been shed, since the discarded armor appears as a complete unit rather than scattered sclerites. In the juvenile that was apparently molting when it died, the feeding apparatus also appears to have been shed, as half of one tooth row is pointing forwards.

Classification

Restoration of *W. corrugata*

During the Cambrian, most of the main groupings of animals recognised today were beginning to diverge. Consequently, many lineages (that would later become extinct) appear intermediate to two or more modern groups, or lack features common to all modern members of a group, and hence fall into the "stem group" of a modern taxon. Debate is ongoing as to whether *Wiwaxia* can be placed within a modern crown group and, if it cannot, in which group's stem it falls. When Walcott first described *Wiwaxia*, he regarded it as a polychaete annelid worm, and its sclerites as similar to the elytra ("scales") of annelids. More recently the debate has been intense, and proposed classifications include: a member of an extinct phylum distantly related to the molluscs; a crown-group polychaete; a stem-group annelid; a problematic bilaterian; a stem- or possibly primitive crown-group mollusc.

In 1985 Simon Conway Morris agreed that there were similarities to polychaetes, but considered that *Wiwaxia*'s sclerites were different in construction to annelids' elytra. He was more impressed by the similarities between *Wiwaxia*'s feeding apparatus and a molluscan radula, and assigned the animal to a new taxon Molluscata, which he proposed should also contain the molluscs and hyolithids. When he later described the first fairly complete specimens of *Halkieria*, he suggested that these were closely related to *Wiwaxia*.

Nick Butterfield, then a postgraduate paleontologist at Harvard inspired by Stephen Jay Gould's lectures, agreed that the sclerites were not like elytra, which are relatively fleshy and soft. However, since the sclerites were solid, he concluded that *Wiwaxia* could not be a member of the "Coeloscleritophora", a taxon that had been proposed in order to unite organisms with hollow sclerites, and could not be closely related to the halkieriids, which have hollow sclerites. Instead he thought that they were very similar in several ways to the chitinous bristles (setae) that project from the bodies of modern annelids and in some genera form leaf-like scales that cover the back like roof tiles – in composition, in detailed structure, in how they were attached to the body via "follicles" and in overall appearance. Some modern annelids also develop on each side rows of longer bristles, which both Walcott and Butterfield considered similar to *Wiwaxia*'s dorsal spines. including the halkieriids.

Butterfield also contended that *Wiwaxia*'s feeding apparatus, instead of being mounted in the middle of its "head", was just as likely to be mounted in two parts on the sides of the "head", an arrangement that is common in polychates. He went so far as to classify *Wiwaxia* as a member of a modern order, Phyllodocida, and pointed out that *Wiwaxia*'s lack of obvious segmentation is no barrier to this, as some modern polychaetes also show no segmentation except during development. He later noted that Wiwaxia lack some polychate features which he would expect to be easily preserved in fossils, and therefore a stem-group annelid, in other words an evolutionary "aunt" of modern annelids.

Conway Morris and Peel (1995) largely accepted Butterfield's arguments and treated *Wiwaxia* as an ancestor or "aunt" of the polychaetes, and said Butterfield had informed them that the microscopic structure of *Wiwaxia*'s sclerites was identical to that of the bristles of two Burgess Shale polychaetes *Burgessochaeta* and *Canadia*. Conway Morris and Peel also wrote that one specimen of *Wiwaxia* showed traces of a small shell, possibly a vestige left over from an earlier stage in the animal's evolution, and noted that one group of modern polychaetes also has what may be a vestigial shell. However they maintained that *Wiwaxia*'s feeding aparatus was much more like a molluscan radula. They also argued that *Wiwaxia* was fairly closely related to and in fact descended from the halkieriids, as the sclerites are divided into similar groups, although those of halkieriids were much smaller and more numerous; they also said that in 1994 Butterfield had found *Wiwaxia* sclerites that were clearly hollow. They presented a large cladogram according to which:

- The earliest halkieriids were a "sister" group to the molluscs, in other words descendants of a fairly closely-related common ancestor.
- The halkieriids which Conway Morris had found in Greenland's Sirius Passet lagerstätte were a "sister" group to brachiopods, animals whose modern forms have bivalve shells but differ from molluscs in having muscular stalks and a distinctive feeding apparatus, the lophophore.
- Another halkieriid genus, Thambetolepis, was a "great aunt" of annelids and *Wiwaxia* was an "aunt" of annelids.

Marine biologist Amélie H. Scheltema *et al.* (2003) argued that *Wiwaxia*'s feeding apparatus is very similar to the radulas of some modern shell-less aplacophoran molluscs, and that the sclerites of the two groups are very similar. They concluded that *Wiwaxia* was a member of a clade that includes molluscs. Scheltema has also highlighted similarities between *Wiwaxia* and the larvae of certain solenogaster molluscs, which bear iterated calcareous sclerites arranged into three symmetrical lateral zones.

Danish zoologist Danny Eibye-Jacobsen argued in 2004 that *Wiwaxia* lacks any characters that would firmly place it as a polychaete or annelid. Eibye-Jacobsen regarded bristles as a feature shared by molluscs, annelids and brachiopods. Hence even if *Wiwaxia*'s sclerites closely resembled bristles, which he doubted, this would not prove that *Wiwaxia*'s closest relative were annelids. He also pointed out that the very different numbers of sclerites in the various zones of *Wiwaxia*'s body do not correspond to any reasonable pattern of segmentation; while Eibye-Jacobsen did not think that this alone would prevent classification of *Wiwaxia* as a polychaete, he thought it was a serious objection given the lack of other clearly polychaete features. In his opinion there were no strong grounds for classifying *Wiwaxia* as a proto-annelid or a proto-mollusc, although he thought the objections against classification as a proto-annelid were the stronger.

Butterfield returned to the debate in 2006, repeating the arguments he presented in 1990 for regarding *Wiwaxia* as an early polychaete and adding that, while bristles are a feature of several groups, they appear as a covering over the back only in polychaetes.

Chapter 11

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

Reconstruction of *Megalosaurus* from 1854, in Crystal Palace, London

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

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, 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.

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 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 they were vegetarians. These features include:

- Jaws that opened only a little and closed so that all the teeth met at the same time
- Large abdomens that could accommodate large amounts of vegetation and store it for the longer time it takes to digest vegetation
- Guts that likely contained Endosymbiotic micro-organisms that 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 mainly feed on grain but may not be essential—and that birds that 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

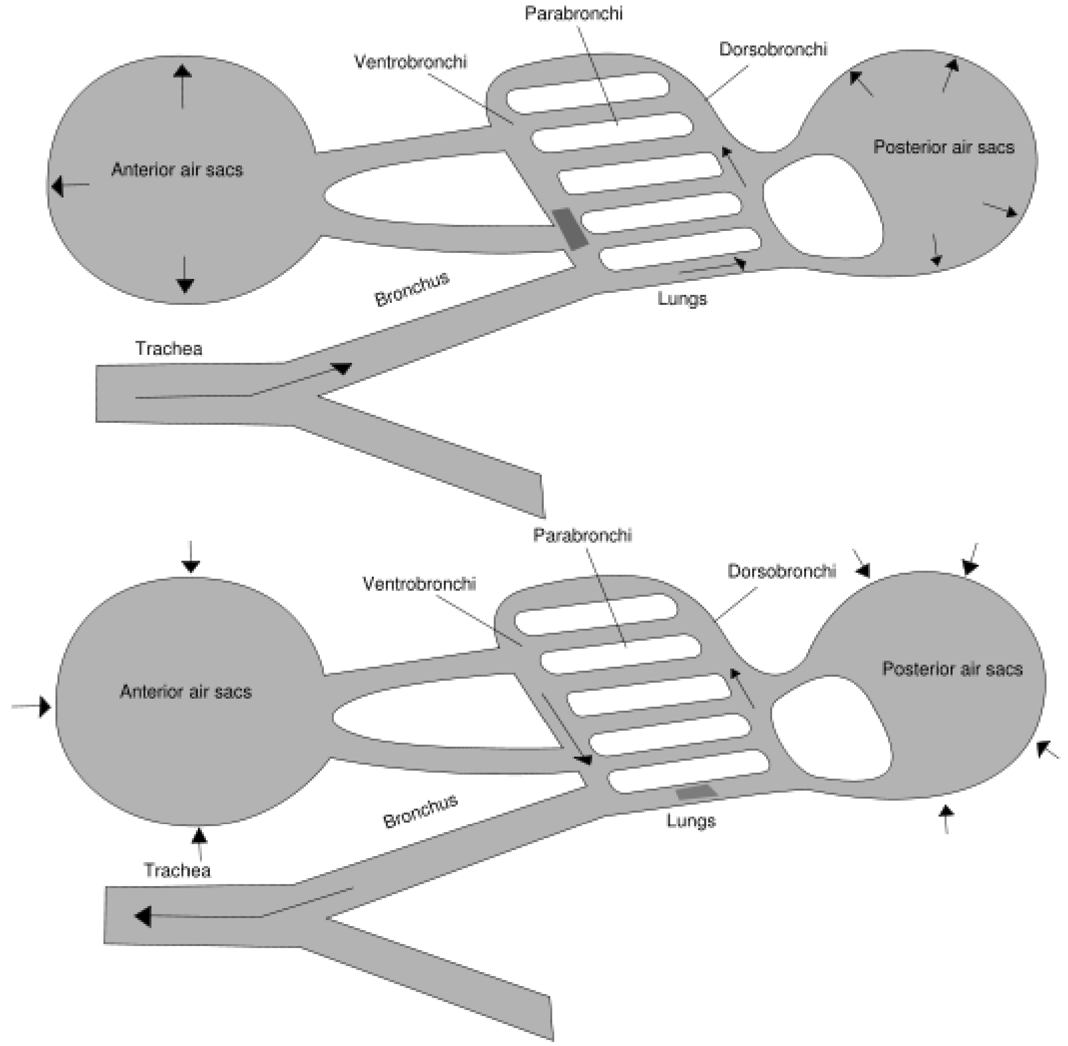
When laying eggs, females of some bird species grow a special type of bone in their limbs between the hard outer bone and the marrow. This medullary bone, which is rich in calcium, is used to make eggshells, and the birds that produced it absorb it when they have finished laying eggs. Medullary bone 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.

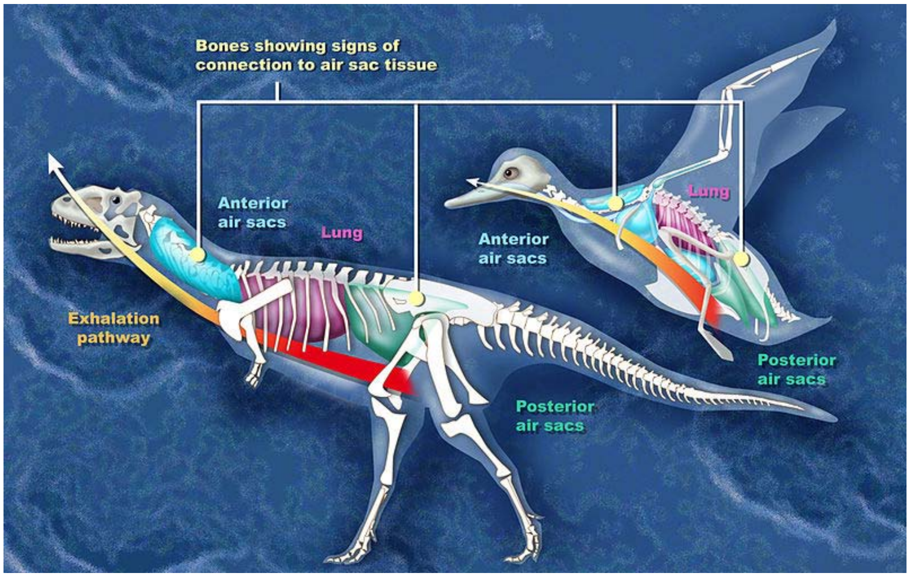
For a long time these cavities were regarded simply as weight-saving devices, but Bakker proposed that they contained air sacs like those that make birds' respiratory systems the most efficient of all animals'.

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:

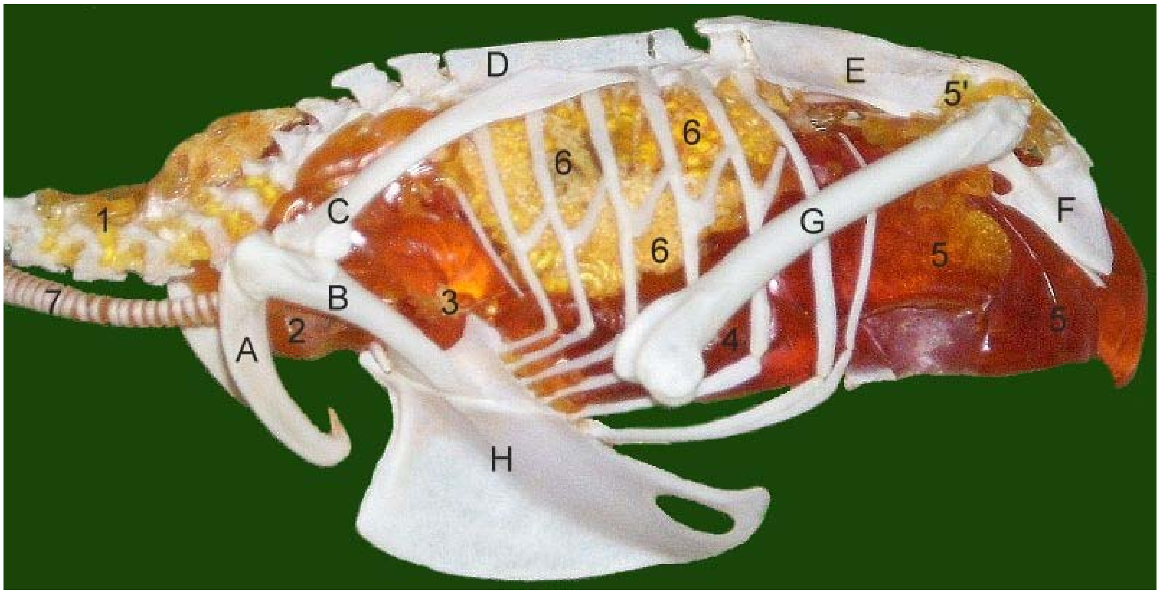
- Increase in respiratory capacity. This is probably the most common hypothesis, and fits well with the idea that many dinosaurs had fairly high metabolic rates.
- Improving balance and maneuvrability by lowering the center of gravity and reducing rotational inertia. However this does not explain the 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

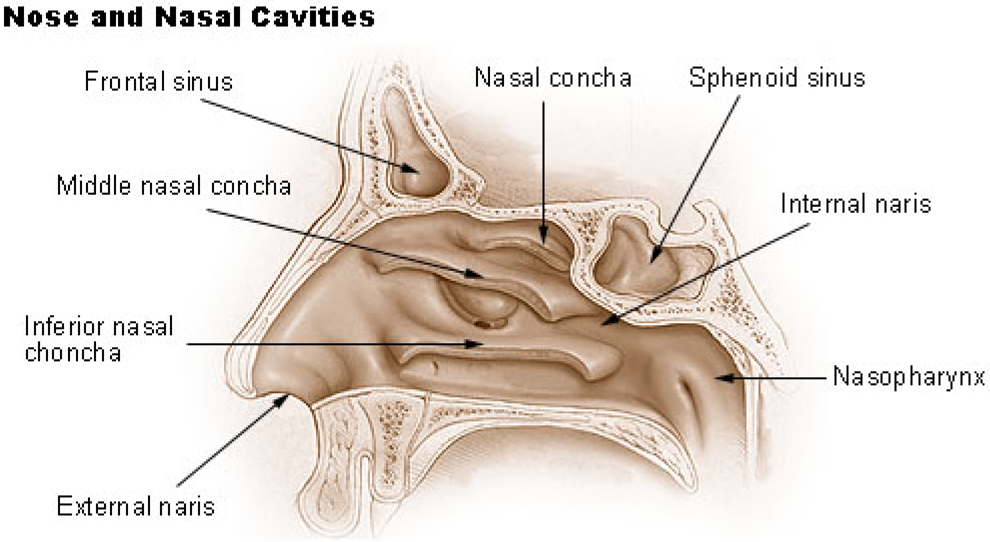
Uncinate processes on the ribs

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, which indicates that maniraptorans needed a high-capacity oxygen supply.

Plates that may have functioned the same way as uncinate processes have been observed 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 that 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.

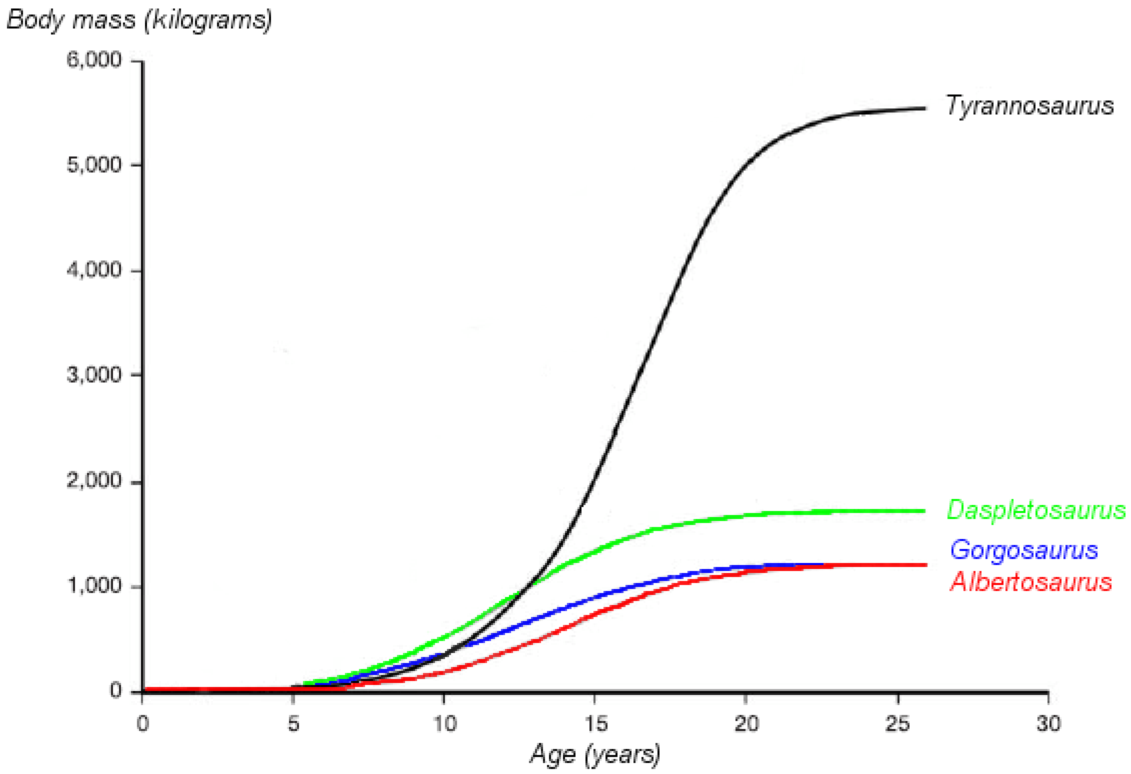
Regardless of the object's identity, it may have little relevance to dinosaurs' internal anatomy and metabolic rate. Both modern crocodilians and birds, the closest living relatives of dinosaurs, have four-chambered hearts, although modified in crocodilians, and so dinosaurs probably had them as well. 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. The activity of metabolic enzymes varies with temperature, so temperature control is vital for any organism, whether endothermic or ectothermic. Organisms can be categorized as poikilotherms (poikilo - changing), which are tolerant of internal temperature fluctuations, and homeotherms (homeo - same), which must maintain a constant core temperature. Animals can be further categorized as endotherms, which regulate their temperature internally, and ectotherms, which regulate temperature by the use of external heat sources.

The current consensus view suggests that dinosaur metabolism did not closely match any found in living vertebrates, and, consequently, that they cannot be categorized as either "warm" or "cold-blooded." Rather, they lie somewhere on the spectrum between poikilothermy and homeothermy. Consequently, current research focuses on mechanisms of metabolism and temperature regulation, and the similarities between dinosaurian, avian and mammalian metabolisms.

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 they needed and allow them to use more of that food for growth than do 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 to facilitate rapid growth and repair damage caused by stress or injuries. Dense secondary Haversian bone, which is formed during remodeling, is found in many living endotherms as well as dinosaurs, pterosaurs and therapsids. Secondary Haversian canals are correlated with size and age, mechanical stress and nutrient turnover. The presence of secondary Haversian canals suggests comparable bone growth and lifespans in mammals and dinosaurs. 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 lines of arrested growth (LAGs), 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. The relationship between LAGs and seasonal growth dependency remains unresolved.

- 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 that examined bone samples from a wide range of archosaurs, including early dinosaurs, and 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.Developing bone found in juveniles is distinctly porous, which has been linked to vascularization and bone deposition rate, all suggesting growth rates close to those observed in modern birds.

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). Studies of the sauropodomorph *Massospondylus* and early theropod *Syntarsus* (*Megapnosaurus*) reveal growth rates of 3 kg/year and 17 kg/year, respectively, much slower than those estimated of Maiasaura and observed in modern birds.

Oxygen isotope ratios in bone

The ratio of the isotopes ^{16}O and ^{18}O in bone depends on the temperature the bone formed at: 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.

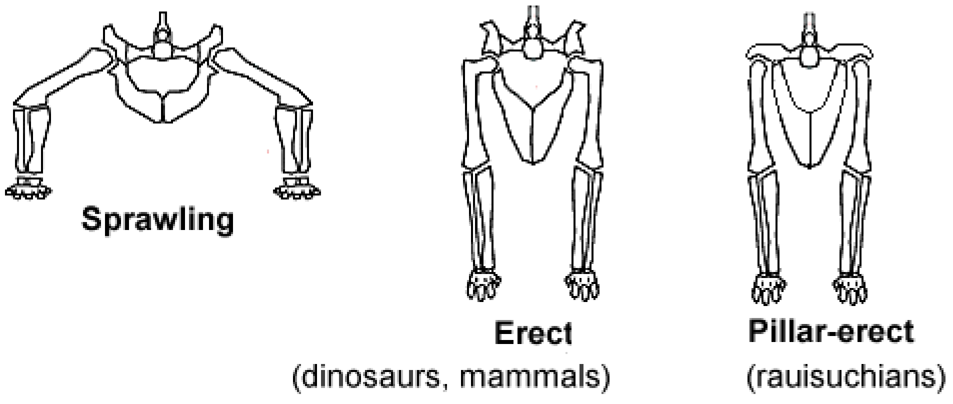
This argument was criticized on several grounds and is no longer taken seriously (the following list of criticisms is far from exhaustive):

- 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 with two lungs that flex their bodies sideways during locomotion find it difficult to move and breathe at the same time. This severely limits 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). However, despite Carrier's constraint, sprawling limbs are efficient for creatures that 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 that 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.

Additionally, an erect posture demands precise balance, the result of a rapidly functioning neuromuscular system. This suggests endothermic metabolism, because an ectothermic animal would be unable to walk or run, and thus to evade predators, when its core temperature was lowered. Other evidence for endothermy includes limb length (many dinosaurs possessed comparatively long limbs) and bipedalism, both found today only in endotherms. Many bipedal dinosaurs possessed gracile leg bones with a short thigh relative to calf length. This is generally an adaptation to frequent sustained running, characteristic of endotherms which, unlike ectotherms, are capable of producing sufficient energy to stave off the onset of anaerobic metabolism in the muscle.

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 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 known dinosaur species. One common interpretation of the plates on stegosaurs' backs is as heat exchangers for thermoregulation, as the plates are filled with blood vessels, which, theoretically, could 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.

Other evidence

Respiration

Endothermy demands frequent respiration, which can result in water loss. In living birds and mammals, water loss is limited by pulling moisture out of exhaled air with mucous-covered respiratory turbinates, tissue-covered bony sheets in the nasal cavity. Several dinosaurs have olfactory turbinates, used for smell, but none have yet been identified with respiratory turbinates.

Brain size

Because endothermy allows refined neuromuscular control, and because brain matter requires large amounts of energy to sustain, some speculate that increased brain size indicates increased activity and, thus, endothermy. The encephalization quotient (EQ) of dinosaurs, a measure of brain size calculated using brain endocasts, varies on a spectrum from bird-like to reptile-like. Using EQ alone, coelosaurs appear to have been as active as living mammals, while theropods and ornithopods fall somewhere between mammals and reptiles, and other dinosaurs resemble reptiles.

The crocodilian puzzle and early archosaur metabolism

It appears that the earliest dinosaurs had the features that form the basis for arguments for warm-blooded dinosaurs—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 implies 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 (see below).

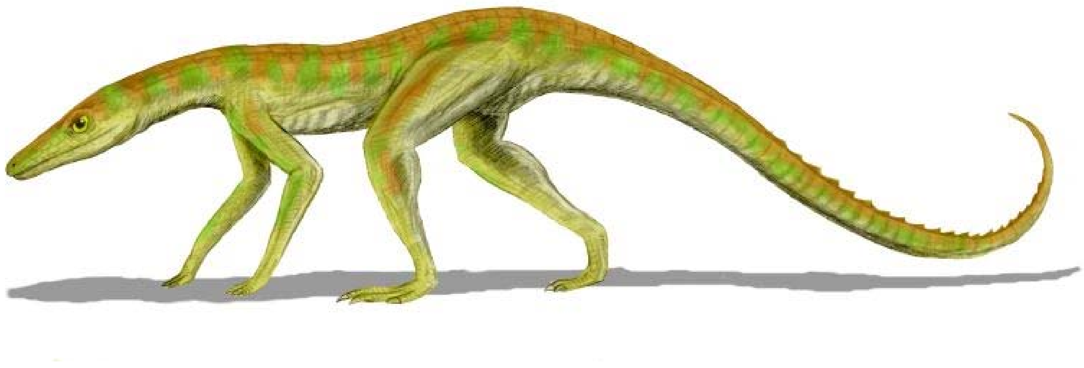
Crocodilians present some puzzles if one regards dinosaurs as active animals with fairly constant body temperatures. Crocodilians evolved shortly before dinosaurs and, second to birds, are dinosaurs' closest living relatives - but modern crocodilians are cold-blooded. This raises some questions:

- 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 can move with their limbs erect, and have several features normally associated with warm-bloodedness because they improve the animal's oxygen supply:

- 4-chambered hearts. Mammals and birds have four-chambered hearts. Non-crocodilian reptiles have three-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 four-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 that makes then functionally three-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 these features, which are important for active warm-blooded creatures but of little apparent use to cold-blooded aquatic ambush predators that spend most 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 indicate that crocodilian embryos develop fully four-chambered hearts first—then develop the modifications that make their hearts function as three-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.