

Transitional Fossils

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Chapter 1

Transitional Fossil



The London specimen of *Archaeopteryx*, discovered only two years after the publication of *On the Origin of Species*.

Transitional fossils (popularly termed **missing links**) are the fossilized remains of intermediary forms of life that illustrate an evolutionary transition. They can be identified

transitional form between dinosaurs and birds. Many more transitional fossils have been discovered since then and it is now considered that there is abundant evidence of how all the major groups of animals are related, much of it in the form of transitional fossils.

Examples

The reconstruction of the evolution of the horse and its relatives assembled by Othniel Charles Marsh from surviving fossils that form a single, consistently developing lineage with many "transitional" types, is often cited as a family tree. However, modern cladistics gives a different, multi-stemmed shrublike picture, with multiple innovations and many dead ends. Other specimens cited as transitional forms include the "walking whale" *Ambulocetus*, the recently-discovered lobe-finned fish *Tiktaalik* and various hominids considered to be proto-humans.

A middle Devonian precursor to seed plants from Belgium has been identified predating the earliest seed plants by about 20 million years. *Runcaria*, small and radially symmetrical, is an integumented megasporangium surrounded by a cupule. The megasporangium bears an unopened distal extension protruding above the multilobed integument. It is suspected that the extension was involved in anemophilous pollination. *Runcaria* sheds new light on the sequence of character acquisition leading to the seed. *Runcaria* has all of the qualities of seed plants except for a solid seed coat and a system to guide the pollen to the seed.

Limitations of the fossil record

Not every transitional form appears in the fossil record because the fossil record is nowhere near complete. Organisms are only rarely preserved as fossils in the best of circumstances and only a fraction of such fossils have ever been discovered. The paleontologist Donald Prothero noted that this is illustrated by the fact that the total number of species of all kinds known through the fossil record was less than 5% of the number of known living species, which suggests that the number of species known through fossils must be less than 1% of all the species that have ever lived. Furthermore the fossil record is very uneven. Certain kinds of organisms, for example those without hard body parts like jellyfish and worms, are very poorly represented.

Evolutionary taxonomy and cladistics

In evolutionary taxonomy, the prevailing form of taxonomy during much of the 20th century and still used in basal textbooks, taxa based on morphological similarity are often drawn as "bubbles" branching off from each other, forming evolutionary trees. Transitional forms, are seen as falling between the various groups in term of anatomy, and are placed at the borders of these.

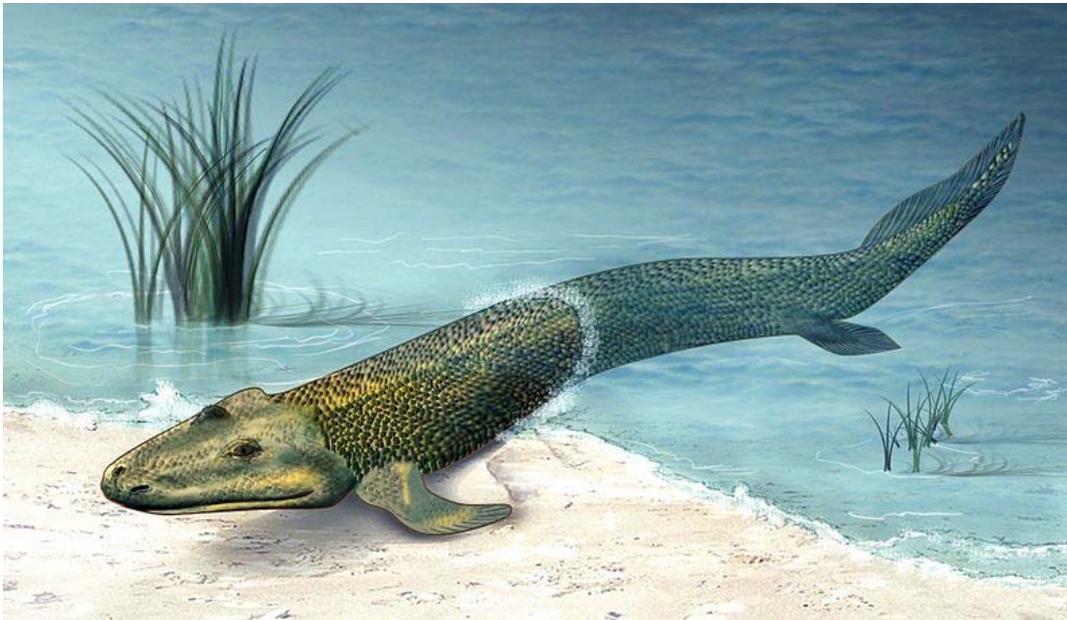
With the establishment of cladistic methods, relationships are now strictly expressed in so-called cladograms, illustrating the branching of the evolutionary lineages. The different so-called 'natural' or 'monophyletic' groups form nested units that do not

overlap. Within cladistics there is thus no longer a transition between established groups, but a differentiation that occurs within groups, represented as a branching in the cladogram. In this context, transitional organisms can be conceptualized as representing early examples on the different branches of a cladogram, lying between a particular branching point and the "crown-group", i.e. the most-derived group, which is placed at the end of a lineage.

Transitional vs ancestral

A source of confusion is the concept that a transitional form between two different taxonomic group must be directly ancestral to one or both groups. This was exacerbated by the fact that one of the goals of evolutionary taxonomy was the attempt to identify taxa that were ancestral to other taxa. However, it is almost impossible to be sure that any form represented in the record is actually a direct ancestor of any other. In fact because evolution is a branching process that produces a complex bush pattern of related species rather than a linear process that produces a ladder like progression, and because of the incompleteness the fossil record, it is unlikely that any particular form represented in the fossil record is a direct ancestor of any other. Cladistics deemphasized the concept of one taxonomic group being an ancestor of another, and instead emphasizes the concept of identifying sister taxa that share a common ancestor with one another more recently than they do with other groups. There are a few exceptional cases, such as some marine plankton micro-fossils, where the fossil record is complete enough to suggest with confidence that certain fossils represent a population that was actually ancestral to another later population, but in general transitional fossils are considered to have features that illustrate the transitional anatomical features of actual common ancestors of different taxa rather than to be actual ancestors.

Comparison to 'intermediate' forms



Life restoration of *Tiktaalik roseae* made for the National Science Foundation

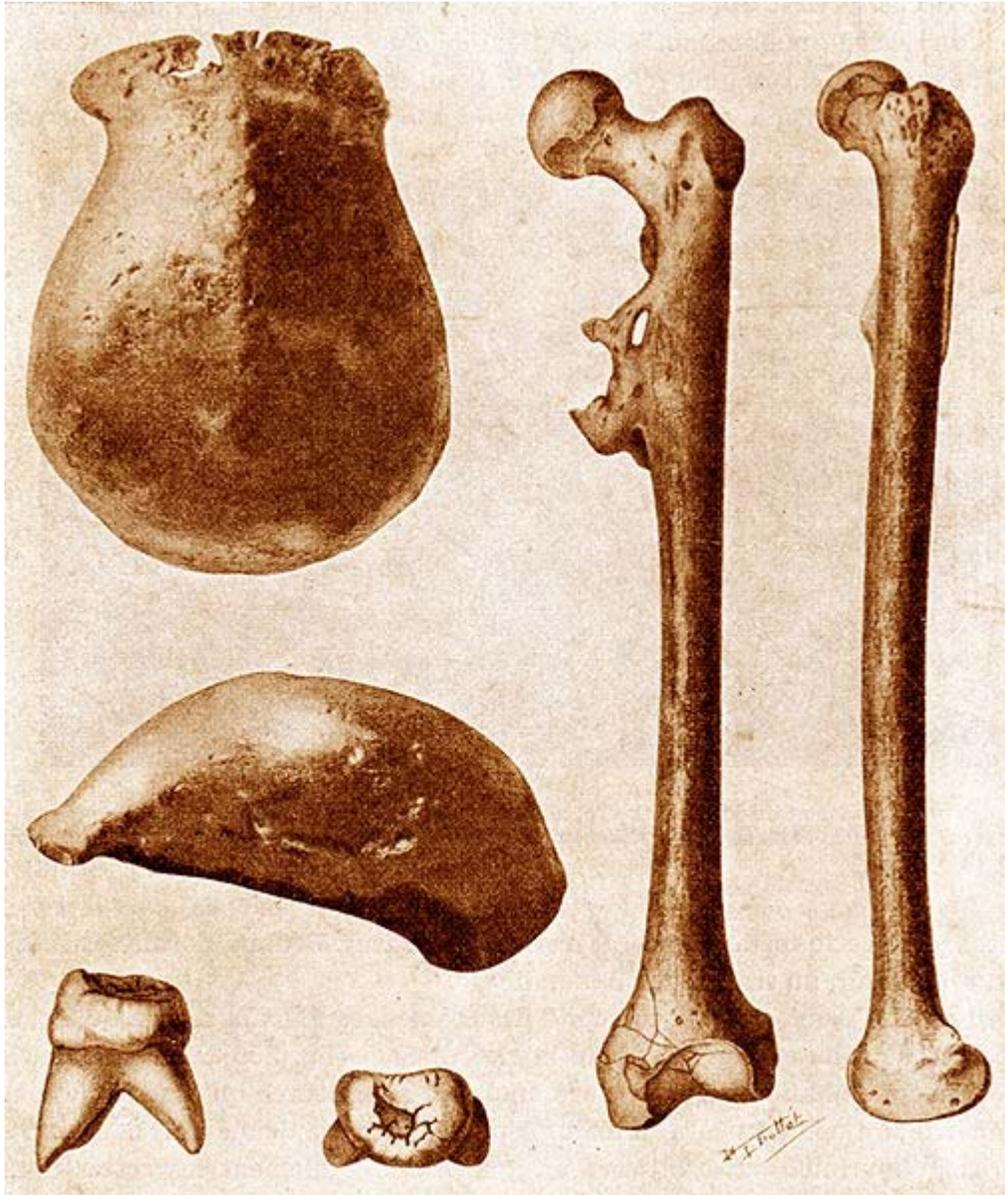
The terms 'transitional' and 'intermediate' are for the most part used as synonyms; however, a distinction between the two can be made:

- "Transitional" can be used for those forms that do *not* have a significant number of unique derived traits that the derived relative does not possess as well. In other words, a transitional organism is morphologically close to the actual common ancestor it shares with its more derived relative.
- "Intermediate" can be used for those forms that *do* have a large number of uniquely derived traits not connected to its derived relative.

According to this definition, *Archaeopteryx*, which does not show any derived traits that more derived birds do not possess as well, is transitional. In contrast, the platypus is intermediate because it retains certain reptilian traits no longer found in modern mammals and also possesses derived traits of a highly specialized aquatic animal.

Following this definition, all living organisms are in fact to be regarded as intermediate forms when they are compared to some other related life-form. Indeed there are many species alive today that can be considered to be transitional between two or more groups.

Missing links



Java Man, widely hailed as the missing link when found in 1891.

A popular term used to designate transitional forms is "missing links". The term tends to be used in the popular media, but is avoided in the scientific press as it relates to the links in the great chain of being, a static pre-evolutionary concept now abandoned. In reality, the discovery of more and more transitional fossils continues to add to knowledge of evolutionary transitions, making many of the "missing links" missing no more.

The term "missing links" was used by Charles Lyell in a somewhat different way in his *Elements of Geology* of 1851, but was popularized in its present meaning by its appearance in Lyell's *Geological Evidences of the Antiquity of Man* of 1863, p. xi. By

that time geologists had abandoned a literal Biblical account and it was generally thought that the end of the last glacial period marked the first appearance of humanity, a view Lyell's *Elements* presented. His *Antiquity of Man* drew on new findings to put the origin of human beings much further back in the deep geological past. Lyell's vivid writing fired the public imagination, inspiring Jules Verne's *Journey to the Center of the Earth*, and Louis Figuier's 1867 second edition of *La Terre avant le déluge* which included dramatic illustrations of savage men and women wearing animal skins and wielding stone axes, in place of the Garden of Eden shown in the 1863 edition.

The idea of a "missing link" between humans and so-called "lower" animals remains lodged in the public imagination. The concept was fuelled by the discovery of *Australopithecus africanus* (Taung Child), Java Man, *Homo erectus*, *Sinanthropus pekinensis* (Peking Man) and other Hominina fossils.

Common creationist arguments

Proponents of creationism have frequently made claims about the existence or implications of transitional fossils that paleontologists consider to be false, and in some cases deliberately misleading. Some of these claims include:

- 'There are no transitional fossils.' This is a claim made by groups like Answers in Genesis and the Institute for Creation Research. Such claims may be based on a misunderstanding of the nature of what represents a transitional feature but are also explained as a tactic actively employed by creationists seeking to distort or discredit evolutionary theory and has been called the "favorite lie" of creationists. Some creationists dispute the lack of transitional forms.
- 'No fossils are found with partially functional features.' Vestigial organs are common in whales (legs), flightless birds (wings), snakes (pelvis and lung), and numerous structures in humans (the coccyx, plica semilunaris, and appendix).
- Henry M. Morris and other creationists have claimed that evolution predicts a continuous gradation in the fossil record, and have misrepresented the expected partial record as having "systematic gaps". Due to the specialized and rare circumstances required for a biological structure to fossilize, only a very small percentage of all life-forms that ever have existed can be expected to be represented in discoveries and each represents only a snapshot of the process of evolution. The transition itself can only be illustrated and corroborated by transitional fossils, but it will never demonstrate an exact half-way point between clearly divergent forms.
- The theory of punctuated equilibrium developed by Stephen Jay Gould and Niles Eldredge and first presented in 1972 is often mistakenly drawn into the discussion of transitional fossils. This theory, however, pertains only to well-documented transitions within taxa or between closely related taxa over a geologically short period of time. These transitions, usually traceable in the same geological outcrop,

often show small jumps in morphology between extended periods of morphological stability. To explain these jumps, Gould and Eldredge envisaged comparatively long periods of genetic stability separated by periods of rapid evolution. Gould made the following observation of creationist misuse of his work to deny the existence of transitional fossils:

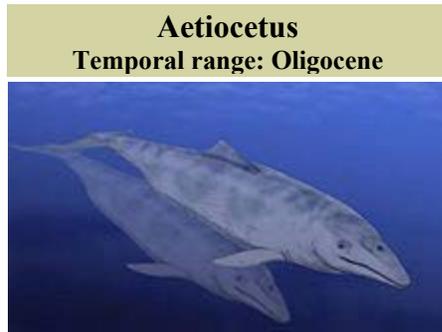
"Since we proposed punctuated equilibria to explain trends, it is infuriating to be quoted again and again by creationists - whether through design or stupidity, I do not know — as admitting that the fossil record includes no transitional forms. The punctuations occur at the level of species; directional trends (on the staircase model) are rife at the higher level of transitions within major groups."

—Stephen Jay Gould, *The Panda's Thumb*

Chapter 2

Aetiocetus and Ambulocetus

Aetiocetus



Aetiocetus cotylalveus

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Cetacea
Suborder:	Mysticeti
Family:	†Aetiocetidae
Genus:	† <i>Aetiocetus</i> Emlong 1966

Type species

A. cotylalveus, Emlong, 1966

Species

- *A. cotylalveus*
- *A. polydentatus*
- *A. tomitai*

- *A. weltoni*

Aetiocetus is an extinct genus of baleen whale that lived 25 million years ago, in the Oligocene period. Its fossils have been found in the North Pacific, around Oregon. It was first named by Douglas Emlong in 1966 and currently contains four species, *A cotylalveus*, *A. polydentatus*, *A. tomitai*, and *A. weltoni*.

Description

Aetiocetus is a transitional fossil between early whales and the modern whales, its blowhole being located halfway up its snout rather than at the top of its head. It is also one of the earliest-known baleen whales. The genus, though more cranially reminiscent of archaic whales, with its pronounced snout and flat cranium, had a loose jaw like later baleen whales. *Aetiocetus* skulls have also shown that the animal bore a full set of teeth, as well as baleen. The skulls contain about forty-four teeth, which consist of cusped molars, curved canines, and incisors. *Aetiocetus* most likely fed on fish and crustaceans.

Douglas Emlong originally classified it in the extinct whale suborder Archaeoceti, because of its teeth. However, when Van Valen analyzed it in 1968, he moved the genus to the suborder Mysticeti due to its derived pattern of bone telescoping.

Species

- *A. cotylalveus*, type species, Emlong, 1966
- *A. polydentatus*, Barnes, Kimura, Furusawa & Sawamura, 1995
- *A. tomitai*, Barnes, Kimura, Furusawa & Sawamura, 1995
- *A. weltoni*, Barnes, Kimura, Furusawa & Sawamura, 1995. An analysis of this species revealed that there were similar palatal nutrient foramina to those which house vessels which feed modern genera of mysticetes.

Sister Taxa

- *Ashorocetus*
- *Chonecetus*
- *Morawanocetus*
- *Willungacetus*

Ambulocetus

Ambulocetus

Temporal range: Early Eocene



Ambulocetus and *Pakicetus* skeletons

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Cetacea
Suborder:	Archaeoceti
Family:	Ambulocetidae
Subfamily:	Ambulocetinae
Genus:	<i>Ambulocetus</i>
Species:	<i>A. natans</i>

Binomial name

Ambulocetus natans

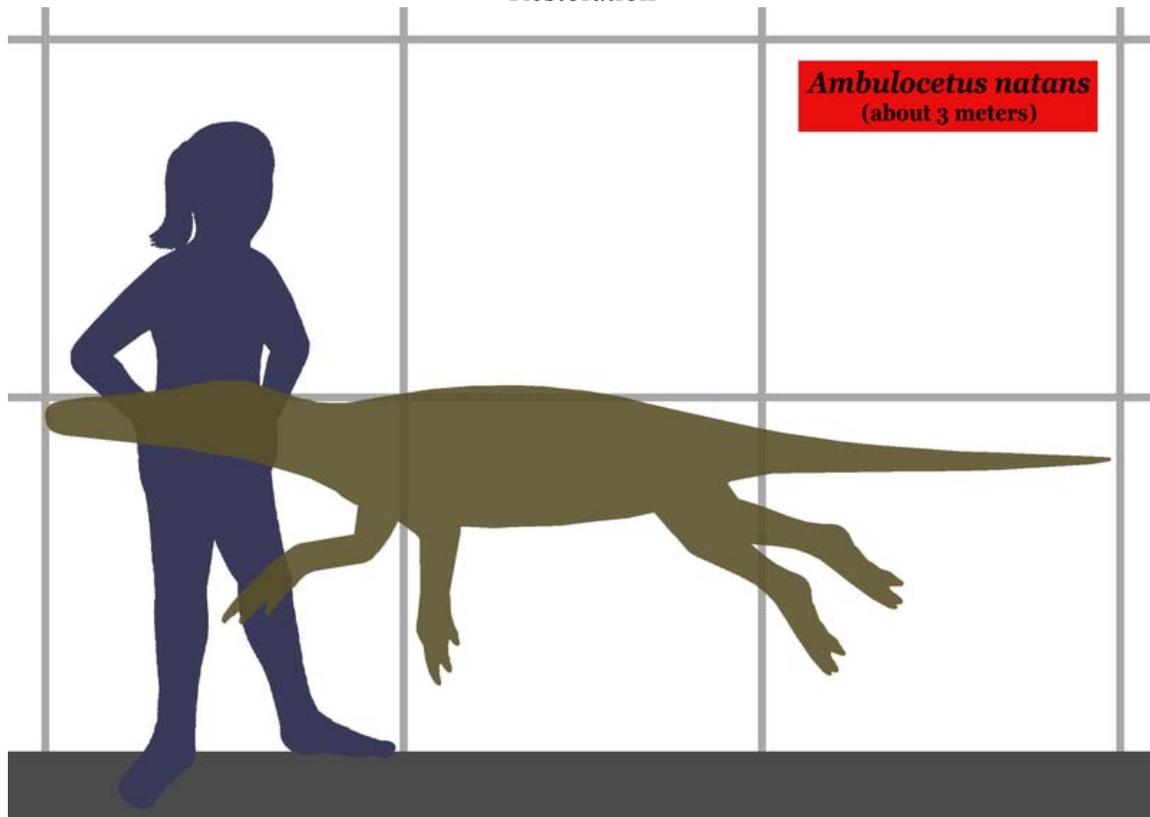
Thewissen et al., 1996

Ambulocetus (or the "walking whale") was an early cetacean that could walk as well as swim. It lived during early Eocene some 50-49 million years ago. It is a transitional fossil that shows how whales evolved from land-living mammals. The *Ambulocetus* fossils were found in Pakistan by anthropologist Johannes Thewissen. When the animal was alive, Pakistan was a coastal region of India, which was then a large island in the Indian Ocean.

Description



Restoration



Ambulocetus size, compared to a human.

Having the appearance of a 3 meter long mammalian crocodile, it was clearly amphibious, as its back legs are better adapted for swimming than for walking on land, and it probably swam by undulating its back vertically, as otters and whales do. It has been speculated that Ambulocetids hunted like crocodiles, lurking in the shallows to

snatch unsuspecting prey. Chemical analysis of its teeth shows that it was able to move between salt and fresh water. *Ambulocetus* did not have external ears. To detect prey on land, they may have lowered their heads to the ground and felt for vibrations.

Scientists consider *Ambulocetus* to be an early whale because it shares underwater adaptations with them: it had an adaptation in the nose that enabled it to swallow underwater, and its periotic bones had a structure like those of whales, enabling it to hear well underwater. In addition, its teeth are similar to those of early cetaceans.

Chapter 3

Anchiornis and Australopithecus

Anchiornis

Anchiornis

Temporal range: Middle Jurassic, 160 Ma



Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Reptilia
Superorder:	Dinosauria
Order:	Saurischia
Suborder:	Theropoda
Family:	†Troodontidae
Genus:	† <i>Anchiornis</i> Xu <i>et al.</i> , 2009

Species

A. huxleyi Xu *et al.*, 2009 (type)

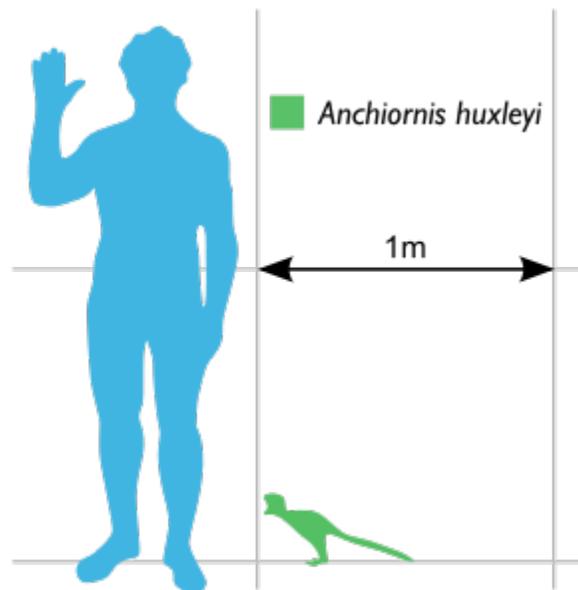
Anchiornis is a genus of small, feathered, troodontid dinosaur. The genus *Anchiornis* contains the type species *Anchiornis huxleyi*, named in honor of Thomas Henry Huxley, an early proponent of biological evolution, and the first to propose a close evolutionary relationship between birds and dinosaurs. The generic name *Anchiornis* means "near

bird", and its describers cited it as important in filling a gap in the transition between the body plans of avian birds and non-avian dinosaurs.

Anchiornis fossils have been found in the Tiaojishan Formation of Liaoning, China, dating somewhat uncertainly to the mid-late Jurassic period (Calloviaian or Oxfordian stage), 160 to 155 million years ago.

Given the exquisite preservation of one of the animal's fossils, *Anchiornis* became the first Mesozoic dinosaur for which almost the entire life coloration could be determined.

Description



Size compared with a human

Anchiornis is a small, early troodontid dinosaur with a triangular skull bearing several details in common with other troodontids. Also like other troodontids, *Anchiornis* had very long legs, usually an indication that it was a strong runner (however, the extensive leg feathers indicate that this may be a vestigial trait, as running animals tend to have reduced, not increased, hair or feathers on their legs). The forelimbs of *Anchiornis* were also very long, unusual among troodontids (which tend to be short-armed) but similar to dromaeosaurids and early birds, emphasizing its basal ("primitive") position among its relatives.

The first fossil was recovered from the Yaolugou locality, Jianchang County, western Liaoning, China; the second, at the Daxishan locality of the same area. The deposits are lake sediment, and are of uncertain age. Radiological measurements indicate an early Late Jurassic age for them, between 161 and 151 million years ago.

Feathers

While the first specimen of *Anchiornis* preserved only faint traces of feathers around the preserved portion of the body, the well-preserved second specimen showed nearly complete feather preservation, allowing researchers to identify the structure of the feathers and how they were distributed.

As in other early paravians such as *Microraptor*, *Anchiornis* had large wings, made up of pennaceous flight feathers attached to the arm and hand (as in modern birds) as well as flight feathers on the hind legs, forming an arrangement of fore and hind wings. The forewing of *Anchiornis* was composed of 11 primary feathers and 10 secondary feathers. Unlike *Microraptor*, the primary feathers in *Anchiornis* were about as long as the secondaries and formed a more rounded wing, with curved but symmetrical central vanes, a small and thin relative size, and rounded tips, all indicating poorer aerodynamic ability compared to its later relative. In *Microraptor* and *Archaeopteryx*, the longest forewing feathers were closest to the tip of the wing, making the wings appear long, narrow, and pointed. However, in *Anchiornis*, the longest wing feathers anchored near the wrist, making the wing broadest in the middle and tapering near the tip for a more rounded, less flight-adapted profile.

The hind wings of *Anchiornis* were also shorter than those of *Microraptor*, and were made up of 12–13 flight feathers anchored to the tibia (lower leg) and 10–11 to the metatarsus (upper foot). Also unlike *Microraptor*, the hind wing feathers were longest closer to the body, with the foot feathers being short and directed downward, almost perpendicular to the foot bones.

Unlike any other known Mesozoic dinosaur, the feet of *Anchiornis* (except for the claws) were completely covered in feathers (much shorter than the ones making up the hind wing).

Two types of simpler, downy (plumaceous) feathers covered the rest of the body, as in *Sinornithosaurus*. Long downy feathers covered almost the entire head and neck, torso, upper legs, and the first half of the tail. The rest of the tail bore pennaceous tail feathers (rectrices).



Artist's impression, illustrating feather arrangement and life coloration

Color

In 2010, a team of scientists examined numerous points among the feathers of an extremely well-preserved *Anchiornis* specimen to survey the distribution of *melanosomes*, the pigment cells that give feathers their color. By studying the types of melanosomes and comparing them with those of modern birds, the scientists were able to map the specific colors and patterning present on *Anchiornis* when it was alive. Though this technique had been used and described for isolated bird feathers and portions of other dinosaurs (such as the tail of *Sinosauroptryx*), *Anchiornis* became the first Mesozoic dinosaur for which almost the entire life coloration was known (note that the tail of this specimen was not preserved).

Most of the body feathers of *Anchiornis* were gray and black. The crown of head feathers was mainly rufous with a gray base and front, and the face had rufous speckles among predominantly black head feathers. The fore and hind wing feathers were white with black tips. The coverts (shorter feathers covering the bases of the long wing feathers) were gray, contrasting the mainly white main wings. The larger coverts of the wing were also white with gray or black tips, forming rows of darker dots along mid-wing. These took the form of dark stripes or even rows of dots on the outer wing (primary feather coverts) but a more uneven array of speckles on the inner wing (secondary coverts). The shanks of the legs were gray other than the long hind wing feathers, and the feet and toes were black.

Paleobiology

Anchiornis is notable for its proportionally long forelimbs, which measured 80% of the total length of the hind limbs. This is similar to the condition in early avians such as *Archaeopteryx*, and the authors pointed out that long forelimbs are necessary for flight. *Anchiornis* also had a more avian wrist than other non-avian theropods. The authors initially speculated that it would have been possible for *Anchiornis* to fly or glide. However, further finds showed that the wings of *Anchiornis*, while well-developed, were short when compared to later species like *Microraptor*, with relatively short primary feathers that had rounded, symmetrical tips, unlike the pointed, aerodynamically proportioned feathers of *Microraptor*.

Anchiornis has hind leg proportions more like those of lower theropod dinosaurs than avialans, with long legs indicating a fast-running lifestyle. However, while long legs normally indicate a fast runner, the legs and even feet and toes of *Anchiornis* were covered in feathers, including long flight feathers similar to those in the hind wings of *Microraptor*, making it unlikely that *Anchiornis* was a capable ground runner.

Like many modern birds, *Anchiornis* exhibited a complex pattern of coloration with different colors in speckled patterns across the body and wings, or "within- and among-feather plumage coloration." In modern birds, such color patterning is used in communication and display, either to members of the same species (e.g. for mating or territorial threat display) or to threaten and warn off competing or predatory species.

History of discovery

The type specimen (in the collection of the Institute of Vertebrate Paleontology and Paleoanthropology, specimen number IVPP V14378) was described by paleontologist Xu Xing and colleagues in a paper accepted to the *Chinese Science Bulletin* in 2009. Xu et al. assigned *Anchiornis* to the Avialae in this paper. The specimen consists of an articulated skeleton missing only the skull, part of the tail, and the right forelimb. The authors estimated that a complete individual would be 34 cm (13 in) and weigh only 110 g (3.9 oz), making it the smallest known non-avian dinosaur.

A second specimen was reported on September 24, 2009, in the journal *Nature*. It is catalogued as number LPM – B00 169 in the Liaoning Paleontological Museum. It is larger and much more complete and preserves long wing feathers on the hands, arms, legs and feet, not unlike *Microraptor*. There is also a feathered crest on the head. This second specimen preserves more features, and led Hu and colleagues to reassign *Anchiornis* to the Troodontidae. A third specimen, preserving a nearly complete skeleton missing the tail and a partial skull, also with extensive feather preservation, was reported in 2010. This third specimen was used to determine the life coloration. It is housed in the Beijing Museum of Natural History with the specimen number BMNHC PH828.

While only three specimens have been formally described, many more have been identified and are held in both private collections and museums. The Shangdong Tianyu

Museum of Nature in Pingyi County, China, for example, was reported to hold 255 specimens of *Anchiornis* in its collections in 2010.

Australopithecus

Gracile australopith

Temporal range: Late Tertiary - Early

Quaternary, 3.9–1.7 Ma

Descendant taxon *Homo* survives to present



Australopithecus afarensis

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Infraclass:	Eutheria
Order:	Primates
Family:	Hominidae
Subfamily:	Homininae
Tribe:	Hominini
Subtribe:	Hominina
Genus:	<i>Australopithecus</i> R.A. Dart, 1925

Species

†*A. africanus*

†*A. garhi*

†*A. sediba*

Also called *Paranthropus*

†*P. aethiopicus*

†*P. robustus*

†*P. boisei*

Also called *Praeanthropus*

†*A. afarensis*

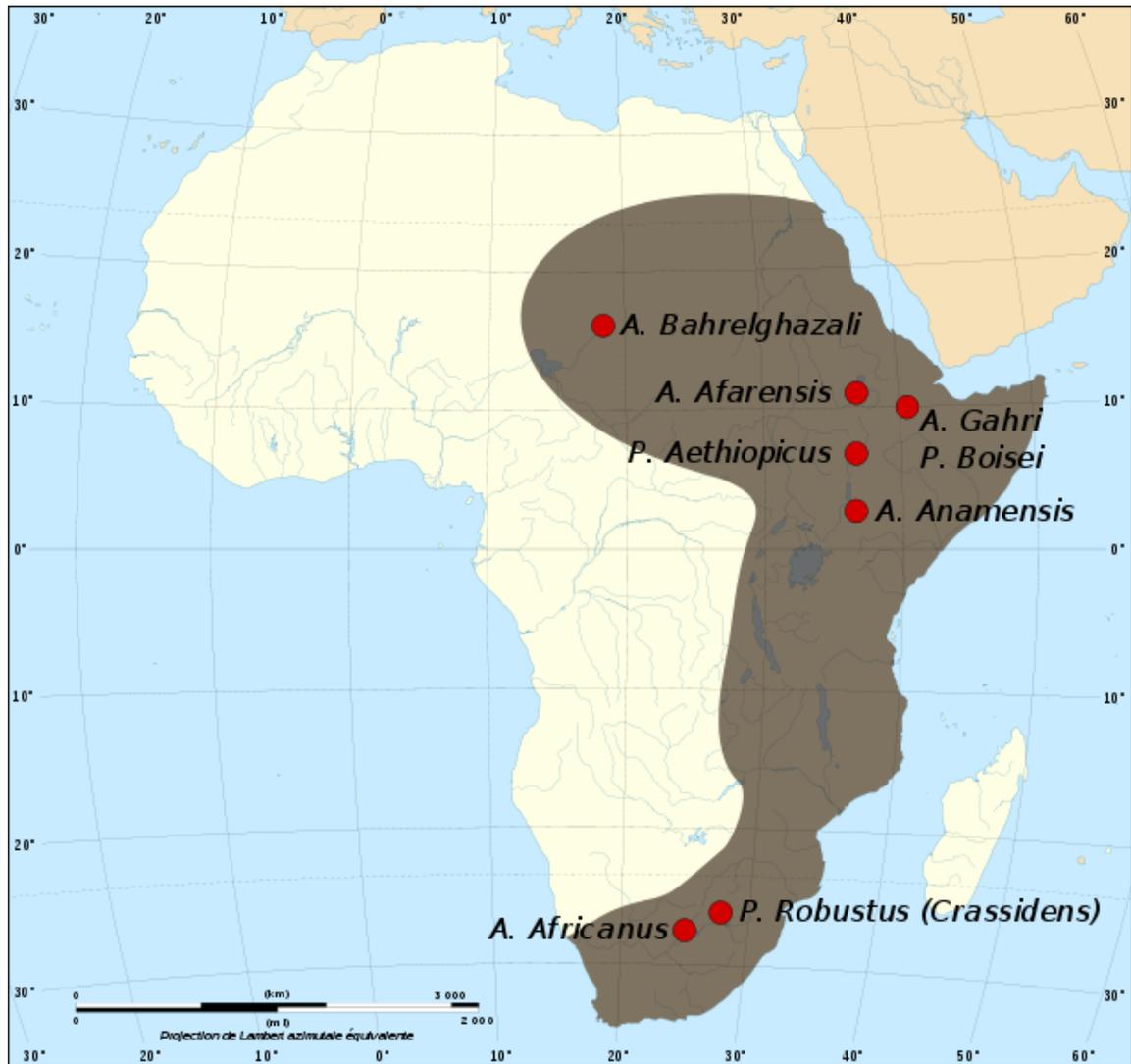
†*A. anamensis*

†*A. bahrelghazali*

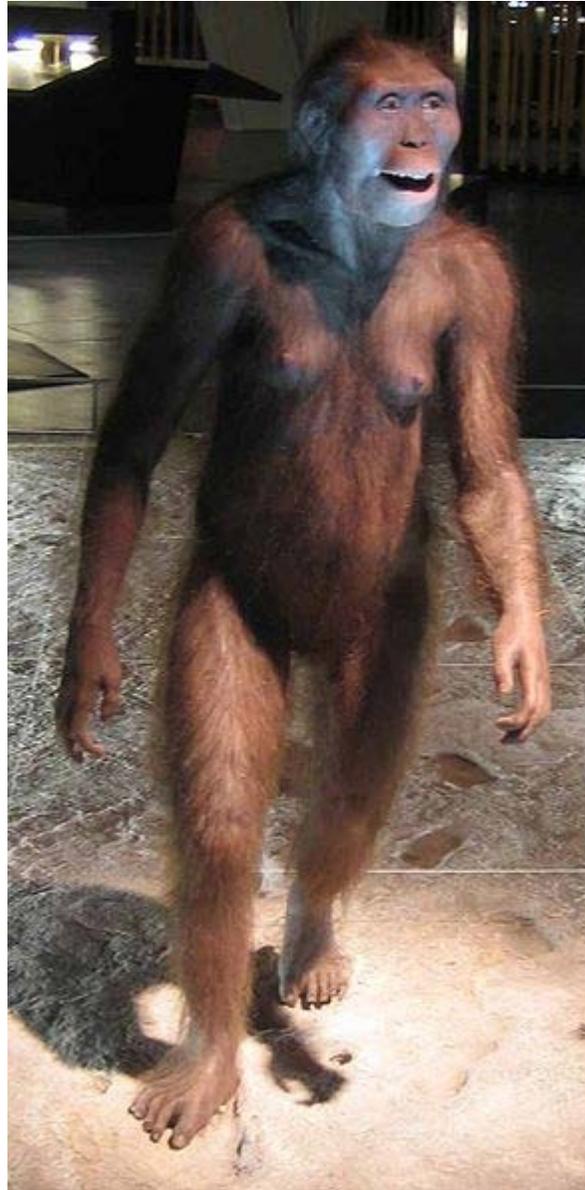
Australopithecus (Latin *australis* "southern", Greek πίθηκος *pithekos* "ape") is a genus of hominids that are now extinct. From the evidence gathered by palaeontologists and archaeologists, it appears that the *Australopithecus* genus evolved in eastern Africa around 4 million years ago before spreading throughout the continent and eventually becoming extinct 2 million years ago. During this time period various different forms of australopiths existed, including *Australopithecus anamensis*, *A. afarensis*, *A. sediba*, and *A. africanus*. There is still some debate amongst academics whether certain African hominid species of this time, such as *A. robustus* and *A. boisei*, constitute members of the same genus; if so, they would be considered to be *robust australopiths* whilst the others would be considered *gracile australopiths*. However, if these species do indeed constitute their own genus, then they may be given their own name, the *Paranthropus*.

It is widely held by archaeologists and palaeontologists that the australopiths played a significant part in human evolution and it was one of the australopith species that eventually evolved into the *Homo* genus in Africa around 2 million years ago, which contained within it species like *Homo habilis*, *H. ergaster* and eventually the modern human species, *H. sapiens sapiens*.

Evolution

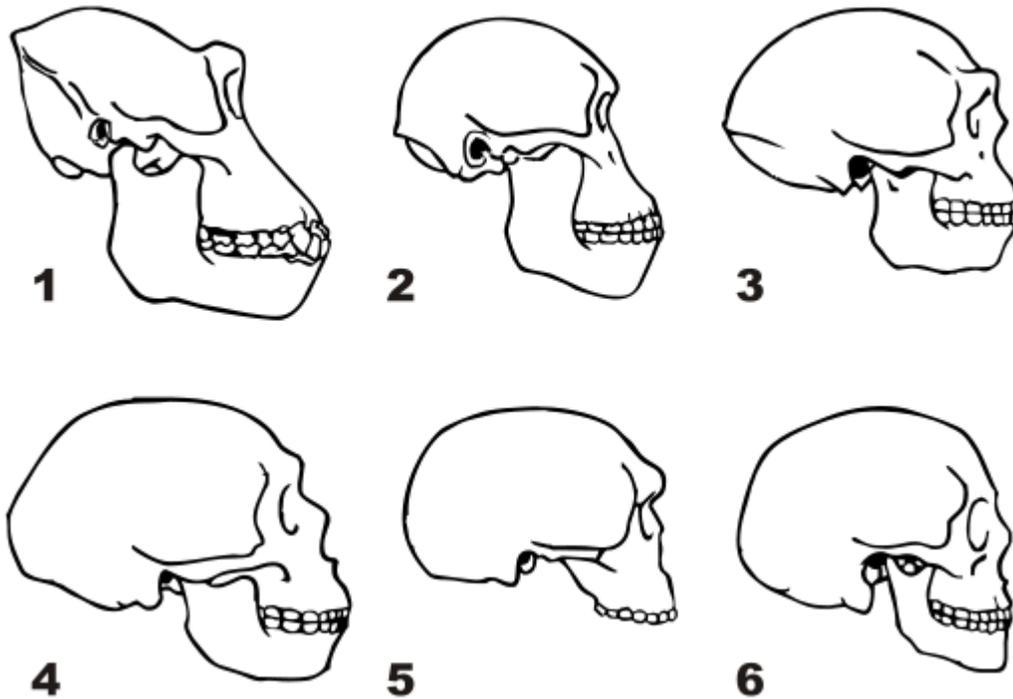


Map of the fossil sites of the early Australopithecines in Africa



Reconstruction of *Australopithecus afarensis*

Gracile australopiths shared several traits with modern apes and humans, and were widespread throughout Eastern and Northern Africa around 3.5 million years ago. The earliest evidence of fundamentally bipedal hominids can be observed at the site of Laetoli in Tanzania. This site contains hominid footprints that are remarkably similar to those of modern humans and have been dated to as old as 3.6 million years. Until recently, the footprints have generally been classified as australopith because that had been the only form of pre-human known to have existed in that region at that time; however, some scholars have considered reassigning them to a yet unidentified very early species of the genus *Homo*.



Craniums

1. Gorilla 2. **Australopithecus** 3. Homo erectus 4. Neanderthal (La Chapelle aux Saints)
5. Steinheim Skull 6. Euhominid

Australopithecus anamensis, *Australopithecus afarensis* and *Australopithecus africanus* are among the most famous of the extinct hominins. *A. africanus* used to be regarded as ancestral to the genus *Homo* (in particular *Homo erectus*). However, fossils assigned to the genus *Homo* have been found that are older than *A. africanus*. Thus, the genus *Homo* either split off from the genus *Australopithecus* at an earlier date (the latest common ancestor being *A. afarensis* or an even earlier form, possibly *Kenyanthropus platyops*), or both developed from a yet possibly unknown common ancestor independently.

According to the Chimpanzee Genome Project, both human (*Ardipithecus*, *Australopithecus* and *Homo*) and chimpanzee (*Pan troglodytes* and *Pan paniscus*) lineages diverged from a common ancestor about 5 to 6 million years ago, if we assume a constant rate of evolution. It is theoretically more likely for evolution to happen more slowly, as opposed to more quickly, from the date suggested by a gene clock (the result of which is given as a "youngest common ancestor", i.e., the latest possible date of diversion.) However, hominins discovered more recently are somewhat older than the molecular clock would theorize. *Sahelanthropus tchadensis*, commonly called "Toumai" is about 7 million years old and *Orrorin tugenensis* lived at least 6 million years ago. Since little is known of them, they remain controversial among scientists since the molecular clock in humans has determined that humans and chimpanzees had an evolutionary split at least a million years later. One theory suggests that the human and

chimpanzee lineages diverged somewhat at first, then some populations interbred around one million years after diverging.

Morphology



Original skull of Mrs. Ples, a male *Australopithecus africanus*

The brains of most species of *Australopithecus* were roughly 35% of the size of that of a modern human brain. Most species of *Australopithecus* were diminutive and gracile, usually standing between 1.2 to 1.4 m tall (approx. 4 to 4.5 feet). In several variations of *Australopithecus* there is a considerable degree of sexual dimorphism, in this case males being larger than females. Modern hominids do not appear to display sexual dimorphism to the same degree — particularly, modern humans display a low degree of sexual dimorphism, with males being only 15% larger than females, on average. In *Australopithecus*, however, males can be up to 50% larger than females. New research suggests that sexual dimorphism may be less pronounced than this, but there is still debate on the subject.

Species variations

Although opinions differ as to whether the species *aethiopicus*, *boisei* and *robustus* should be included within the genus *Australopithecus*, the current consensus in the scientific community is that they should be placed in a distinct genus, *Paranthropus*, which is believed to have developed from the ancestral *Australopithecus* line. Up until

the last half-decade, the majority of the scientific community included all the species shown in the box at the top of single genus. However, *Paranthropus* was morphologically distinct from *Australopithecus*, and its specialized morphology also implies that its behavior was quite different from that of its ancestors.

Evolutionary role



Cast of the skeleton of Lucy, an *Australopithecus afarensis*

The fossil record seems to indicate that *Australopithecus* is the common ancestor of the distinct group of hominids, now called *Paranthropus* (the "robust australopiths"), and most likely the genus *Homo* which includes modern humans. Although the intelligence of these early hominids was likely no more sophisticated than modern apes, the bipedal stature is the key evidence which distinguishes the group from previous primates who are

quadrupeds. The morphology of *Australopithecus* upsets what scientists previously believed, namely, that large brains preceded bipedalism. If *A. afarensis* was the definite hominid which left the footprints at Laetoli, it strengthens the notion that *A. afarensis* had a small brain but was a biped. Fossil evidence such as this has made it clear that bipedalism far predated large brains. However, it remains a matter of controversy how bipedalism first evolved millions of years ago (several concepts are still being studied). The advantages of bipedalism allowed hands to be free for grasping objects (e.g. carrying food and young), and allowed the eyes to look over tall grasses for possible food sources or predators. However, many anthropologists argue that these advantages were not large enough to cause the evolution of bipedalism.



Skull of the Taung child

A recent study of primate evolution and morphology noted that all apes, both modern and fossil, show skeletal adaptations to upright posture of the trunk, and that fossils such as *Orrorin tugenensis* indicate bipedalism around 6 million years ago, around the time of the split between humans and chimpanzees indicated by genetic studies. This suggested that upright, straight-legged walking originally evolved as an adaptation to tree-dwelling. Studies of modern orangutans in Sumatra showed that these apes use four legs when walking on large stable branches, swing underneath slightly smaller branches, but are bipedal and keep their legs very straight when walking on multiple small flexible branches under 4 cm. diameter, while also using their arms for balance and additional

support. This enables them to get nearer to the edge of the tree canopy to get fruit or cross to another tree.

It is suggested that the ancestors of gorillas and chimpanzees became more specialised in climbing vertical tree trunks, using a bent hip and bent knee posture which matches the knuckle-walking posture they use for ground travel. This was due to climate changes around 11 to 12 million years ago that affected forests in East and Central Africa so that there were periods when openings prevented travel through the tree canopy, and at these times ancestral hominids could have adapted the upright walking behaviour for ground travel. Humans are closely related to these apes, and share features including wrist bones apparently strengthened for knuckle-walking. The view that human ancestors were knuckle-walkers is now questioned since the anatomy and biomechanics of knuckle-walking in chimpanzees and gorillas are different suggesting two separate evolutions that happened after the last common ancestor with the human lineage. Further comparative analysis with other primates suggests these wrist bone adaptations support a palm based tree walking.

Radical changes in morphology took place before gracile australopiths evolved; the pelvis structure and feet are very similar to modern humans. The teeth have small canines, but australopiths generally evolved a larger post-canine dentition with thicker enamel.

Most species of *Australopithecus* were not any more adept at tool use than modern non-human primates, yet modern African apes, chimpanzees, and most recently gorillas, have been known to use simple tools (i.e. cracking open nuts with stones and using long sticks to dig for termites in mounds), and chimpanzees have been observed using spears (not thrown) for hunting. However, some have argued that *A. garhi* used stone tools due to a loose association of this species and butchered animal remains.

Diet

In a 1979 preliminary microwear study of *Australopithecus* fossil teeth, anthropologist Alan Walker theorized that robust australopiths were largely frugivorous. Much research has focused on a comparison between the South African species *Australopithecus africanus* and *Paranthropus robustus*. Early analyses of dental microwear in these two species showed that compared to *Paranthropus robustus*, *Australopithecus africanus* had fewer microwear features and more scratches as opposed to pits on its molar wear facets. These observations have been interpreted as evidence that *Paranthropus robustus* may have fed on hard and brittle foods like some nuts and seeds. More recently new analyses based on three-dimensional renderings of wear facets have confirmed earlier work but have also suggested that *Paranthropus robustus* ate hard foods primarily as a fallback resource while *Australopithecus africanus* ate more mechanically tough foods.

In 1992, trace element studies of the strontium/calcium ratios in robust australopith fossils suggested the possibility of animal consumption, as they did in 1994 using stable carbon isotopic analysis. *Australopithecus* mainly ate fruit, vegetables, and tubers.

History of study

The first australopithecine to be discovered and documented was a fossil of a three year old *Australopithecus africanus* which was discovered in a lime quarry by workers at Taung, South Africa. The specimen was studied by the Australian anatomist Raymond Dart, who was then working at the University of the Witwatersrand in Johannesburg who published his findings in *Nature* magazine in February 1925. Dart realised that the fossil contained a number of humanoid features, and so came to the conclusion that this was an early ancestor of humans. Ten years later, he and the Scottish paleontologist Robert Broom, set about to search for more early hominin specimens, and at several sites they found further *A. africanus* remains as well as fossils of a species which Broom named *Paranthropus* (which would now be recognised as *Paranthropus robustus*). Initially, anthropologists were largely hostile to the idea that these discoveries were anything but apes, though this changed during the latter years of the 1940s.

The first australopithecine to be discovered in eastern Africa was a skull belonging to an *Australopithecus bosei* that was excavated in 1959 in the Olduvai Gorge in Tanzania by Mary Leakey. Since then, the Leakey family have continued to excavate the gorge, uncovering further evidence for australopithecines as well as for *Homo habilis* and *Homo erectus*.

Scientists have recently discovered a new australopithecine in South Africa. The fossils of "Australopithecus sediba", which lived 1.9 million years ago, were found in Malapa cave in South Africa. It is thought "Australopithecus africanus" probably gave rise to "Australopithecus sediba", which some scientists think possibly evolved into "Homo erectus".

Chapter 4

Archaeopteryx

Archaeopteryx

Temporal range: Late Jurassic, 150.8–
148.5 Ma



The Berlin *Archaeopteryx*

Scientific classification [e]

Kingdom: Animalia

Phylum: Chordata

Class: Aves

Order: †Archaeopterygiformes

Family: †Archaeopterygidae

Genus: †*Archaeopteryx*
Meyer, 1861

Species: †*A. lithographica*
Meyer, 1861 [*nomen conservandum*]

Synonyms

Archaeopteryx crassipes Meyer, 1887
(Ostrom, 1972) [originally *Pterodactylus nomen rejectum*]
Griphosaurus problematicus Wagner, 1862 [*nomen rejectum*]
Griphornis longicaudatus Woodward, 1862 [*nomen rejectum*]
Archaeopteryx macrura Owen, 1862 [*nomen rejectum*]
Archaeornis siemensii (Dames, 1897) Petronievics, 1917 [originally *Archaeopteryx*]
Archaeopteryx owenii Petronievics, 1917 [*nomen rejectum*]
Jurapteryx recurva? (Howgate, 1985) Howgate, 1984 [originally *Archaeopteryx*]
Wellnhoferia grandis? Elzanowski, 2001

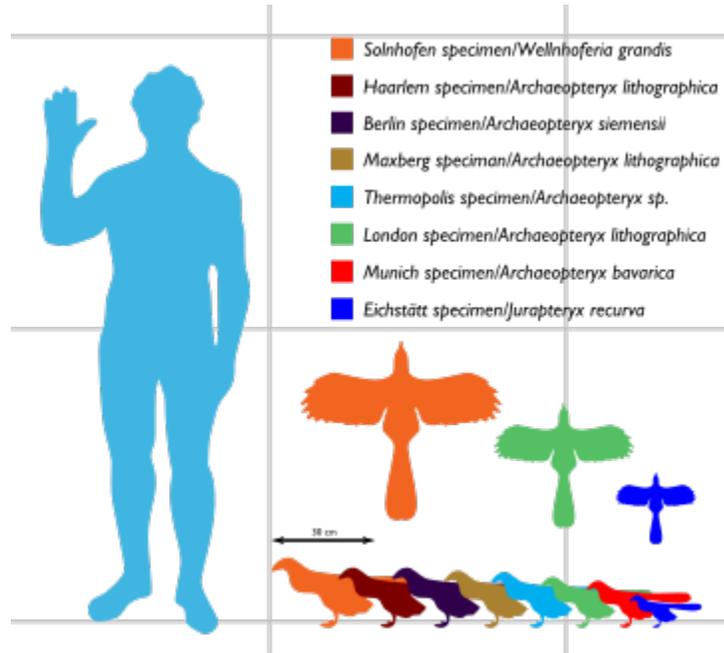
Archaeopteryx is the earliest and most primitive bird known. The name derives from the Ancient Greek ἀρχαῖος (*archaios*) meaning "ancient", and πτέρυξ (*pteryx*), meaning "feather" or "wing".

Archaeopteryx lived in the Late Jurassic Period around 150 million years ago, in what is now southern Germany during a time when Europe was an archipelago of islands in a shallow warm tropical sea, much closer to the equator than it is now.

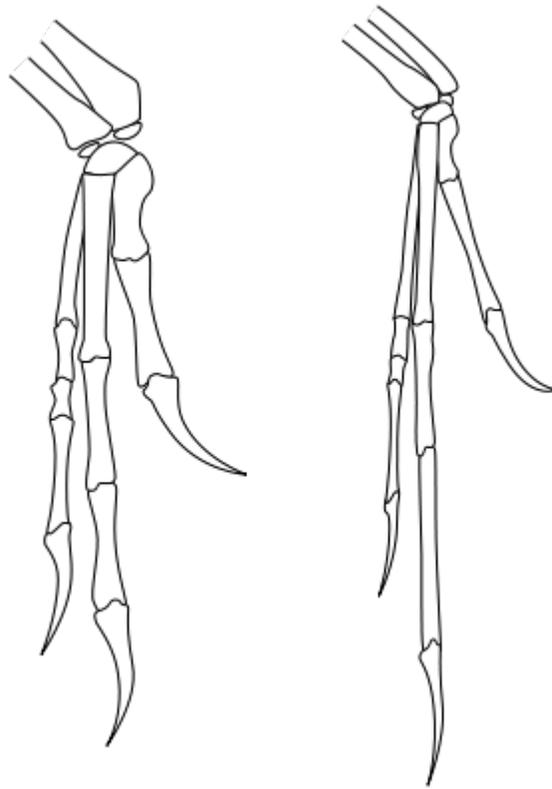
Similar in shape to a European Magpie, and possibly the size of a raven, *Archaeopteryx* could grow to about 0.5 metres (1.6 ft) in length. Despite its small size, broad wings, and inferred ability to fly or glide, *Archaeopteryx* has more in common with small theropod dinosaurs than it does with modern birds. In particular, it shares the following features with the deinonychosaurs (dromaeosaurs and troodontids): jaws with sharp teeth, three fingers with claws, a long bony tail, hyperextensible second toes ("killing claw"), feathers (which also suggest homeothermy), and various skeletal features. The features above make *Archaeopteryx* a clear candidate for a transitional fossil between dinosaurs and birds. Thus, *Archaeopteryx* plays an important role not only in the study of the origin of birds but in the study of dinosaurs. It was named from a feather in 1861. That same year, the first complete specimen of *Archaeopteryx* was announced; this was only two years after Charles Darwin published *On the Origin of Species*, and it became a key piece of evidence in the debate over evolution. Over the years, nine more fossils of *Archaeopteryx* have surfaced. Despite variation among these fossils, most experts regard all the remains that have been discovered as belonging to a single species, though this is still debated.

Many of these eleven fossils include impressions of feathers—among the oldest direct evidence of such structures. Moreover, because these feathers are an advanced form (flight feathers), these fossils are evidence that the evolution of feathers began before the Late Jurassic.

Description



Eight specimens compared to a human in scale.



Comparison of forelimbs of *Deinonychus* (left) and *Archaeopteryx* (right), one of many skeletal similarities between birds and dromaeosaurids.

Archaeopteryx was a primitive bird that lived during the early Tithonian stage of the Jurassic Period, around 150.8–148.5 million years ago. The only specimens of *Archaeopteryx* that have been discovered come from the Solnhofen limestone in Bavaria, southern Germany, which is a *lagerstätte*, a rare and remarkable geological formation known for its superbly detailed fossils.

Archaeopteryx was roughly the size of a raven, with broad wings that were rounded at the ends and a long tail compared to its body length. It could reach up to 500 millimetres (20 in) in body length, with an estimated weight of 0.8 to 1 kilogram (1.8 to 2.2 lb). *Archaeopteryx* feathers, although less documented than its other features, were very similar in structure and design to modern-day bird feathers. However, despite the presence of numerous avian features, *Archaeopteryx* had many theropod dinosaur characteristics. Unlike modern birds, *Archaeopteryx* had small teeth as well as a long bony tail, features which *Archaeopteryx* shared with other dinosaurs of the time.

Because it displays a number of features common to both birds and dinosaurs, *Archaeopteryx* has often been considered a link between them—possibly the first bird in its change from a land dweller to a bird. In the 1970s, John Ostrom, following T. H. Huxley's lead in 1868, argued that birds evolved within theropod dinosaurs and *Archaeopteryx* was a critical piece of evidence for this argument; it had a number of avian features, such as a wishbone, flight feathers, wings and a partially reversed first toe, and a number of dinosaur and theropod features. For instance, it has a long ascending process of the ankle bone, interdental plates, an obturator process of the ischium, and long chevrons in the tail. In particular, Ostrom found that *Archaeopteryx* was remarkably similar to the theropod family Dromaeosauridae.

The first remains of *Archaeopteryx* were discovered in 1861; just two years after Charles Darwin published *On the Origin of Species*. *Archaeopteryx* seemed to confirm Darwin's theories and has since become a key piece of evidence for the origin of birds, the transitional fossils debate, and confirmation of evolution. Indeed, further research on dinosaurs from the Gobi Desert and China has since provided more evidence of a link between *Archaeopteryx* and the dinosaurs, such as the Chinese feathered dinosaurs. *Archaeopteryx* is close to the ancestry of modern birds, and it shows most of the features one would expect in an ancestral bird. However, it may not be the direct ancestor of living birds, and it is uncertain how much evolutionary divergence was already present among other birds at the time.

Paleobiology

Plumage



1880 photo of the Berlin *Archaeopteryx* specimen, showing leg feathers that were subsequently removed during preparation

Specimens of *Archaeopteryx* were most notable for their well-developed flight feathers. They were markedly asymmetrical and showed the structure of flight feathers in modern birds, with vanes given stability by a barb-barbule-barbicel arrangement. The tail feathers were less asymmetrical, again in line with the situation in modern birds and also had firm vanes. The thumb, however, did not yet bear a separately movable tuft of stiff feathers.

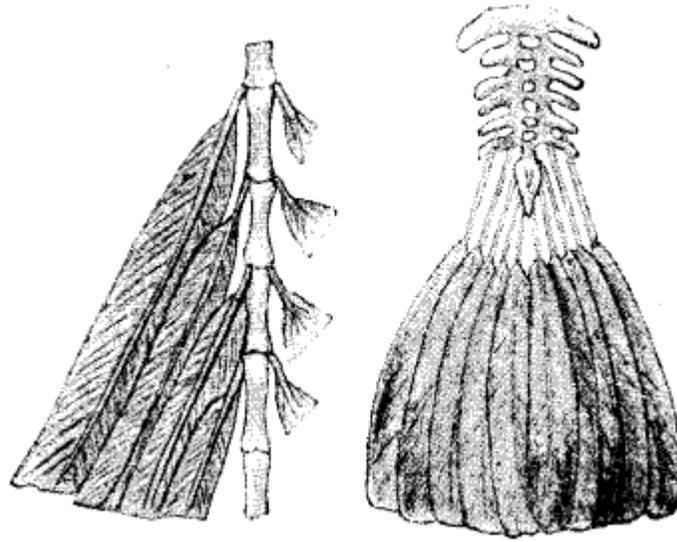
The body plumage of *Archaeopteryx* is less well documented and has only been properly researched in the well-preserved Berlin specimen. Thus, as more than one species seems to be involved, the research into the Berlin specimen's feathers does not necessarily hold true for the rest of the species of *Archaeopteryx*. In the Berlin specimen, there are "trousers" of well-developed feathers on the legs; some of these feathers seem to have a basic contour feather structure but are somewhat decomposed (they lack barbicels as in ratites). However, in part they are firm and thus capable of supporting flight.

There was a patch of pennaceous feathers running along the back which was quite similar to the contour feathers of the body plumage of modern birds in being symmetrical and firm, though not as stiff as the flight-related feathers. Apart from that, the feather traces in the Berlin specimen are limited to a sort of "proto-down" not dissimilar to that found in the dinosaur *Sinosauropteryx*, being decomposed and fluffy, and possibly even appeared more like fur than like feathers in life (though not in their microscopic structure). These occur on the remainder of the body, as far as such structures are both preserved and not obliterated by preparation, and the lower neck.

However, there is no indication of feathering on the upper neck and head. While these may conceivably have been nude, this may still be an artifact of preservation. It appears that most *Archaeopteryx* specimens became embedded in anoxic sediment after drifting some time on their back in the sea—the head and neck and the tail are generally bent downwards, which suggests that the specimens had just started to rot when they were embedded, with tendons and muscle relaxing so that the characteristic shape of the fossil specimens was achieved. This would mean that the skin was already softened and loose, which is bolstered by the fact that in some specimens the flight feathers were starting to detach at the point of embedding in the sediment. So it is hypothesized that the pertinent specimens moved along the sea bed in shallow water for some time before burial, the head and upper neck feathers sloughing off, while the more firmly attached tail feathers remained.

Flight

As in the wings of modern birds, the flight feathers of *Archaeopteryx* were somewhat asymmetrical and the tail feathers were rather broad. This implies that the wings and tail were used for lift generation. However, it is unclear whether *Archaeopteryx* was simply a glider or capable of flapping flight. The lack of a bony breastbone suggests that *Archaeopteryx* was not a very strong flier, but flight muscles might have attached to the thick, boomerang-shaped wishbone, the platelike coracoids, or perhaps to a cartilaginous sternum. The sideways orientation of the glenoid (shoulder) joint between scapula, coracoid and humerus—instead of the dorsally angled arrangement found in modern birds—suggests that *Archaeopteryx* was unable to lift its wings above its back, a requirement for the upstroke found in modern flapping flight. Thus, it seems likely that *Archaeopteryx* was indeed unable to use flapping flight as modern birds do, but it may well have utilized a downstroke-only flap-assisted gliding technique.



Anatomical illustration comparing the "frond-tail" of *Archaeopteryx* with the "fan-tail" of a modern bird

Archaeopteryx wings were relatively large, which would have resulted in a low stall speed and reduced turning radius. The short and rounded shape of the wings would have increased drag, but could also have improved *Archaeopteryx*' ability to fly through cluttered environments such as trees and brush (similar wing shapes are seen in birds which fly through trees and brush, such as crows and pheasants). The presence of "hind wings", asymmetrical flight feathers stemming from the legs similar to those seen in dromaeosaurids such as *Microraptor*, would also have added to the aerial mobility of *Archaeopteryx*. The first detailed study of the hind wings by Longrich in 2006 suggested that the structures formed up to 12% of the total airfoil. This would have reduced stall speed by up to 6% and turning radius by up to 12%.

The feathers of *Archaeopteryx* were asymmetrical. This has been interpreted as evidence that it was a flyer, as flightless birds tend to have symmetrical feathers. However, some scientists, including Thomson and Speakman, have questioned this. They studied more than 70 families of living birds, and found that some flightless types do have a range of asymmetry in their feathers, and that the feathers of *Archaeopteryx* fall into this range.

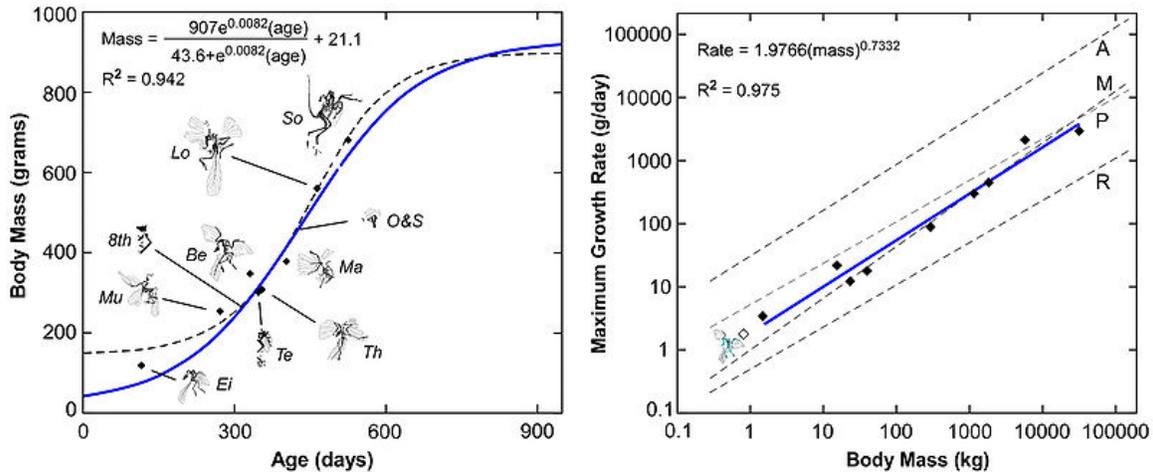
In 2010, Robert L. Nudds and Gareth J. Dyke in the journal *Science* published a paper in which they analysed the rachises of the primary feathers of *Confuciusornis* and *Archaeopteryx*. The analysis suggested that the rachises on these two genera were thinner and weaker than those compared to modern birds relative to body weight. The authors determined that *Archaeopteryx*, along with *Confuciusornis*, were unable to use flapping flight. This study, however, was criticized by Currie and Luis Chiappe. Chiappe suggested that it is difficult to measure the rachises of fossilized feathers, and Currie speculated that *Archaeopteryx* and *Confuciusornis* must have been able to fly to some degree, as their fossils are preserved in what is believed to have been in marine or lake sediments, suggesting that they must have been able to fly over deep water. Gregory Paul

also disagreed with the study, arguing in a 2010 response that Nudds and Dyke had overestimated the weights of these early birds, and that more accurate weight estimates allowed powered flight even with relatively narrow rachises. Nudds and Dyke had assumed a weight of 250 grams for the Munich specimen *Archaeopteryx*, a young juvenile, based on published weight estimates of larger specimens. Paul argued that a more reasonable body weight estimate for the Munich specimen is about 140 grams. Paul also criticized the measurements of the rachises themselves, noting that the feathers in the Munich specimen are poorly preserved. Nudds and Dyke reported a diameter of .75 millimetres (0.030 in) for the longest primary feather, which Paul could not confirm using photographs. Paul measured some of the inner primary feathers, finding rachises 1.25-1.4 mm across. Despite these criticisms, Nudds and Dyke stood by their original conclusions. They claimed that Paul's statement that an adult *Archaeopteryx* would have been a better flyer than the juvenile Munich specimen was dubious. This, they reasoned, would require even thicker rachis, evidence for which has not yet been presented.

In 2004, scientists analyzing a detailed CT scan of the braincase of *Archaeopteryx* concluded that its brain was significantly larger than that of most dinosaurs, indicating that it possessed the brain size necessary for flying. The overall brain anatomy was reconstructed using the scan. The reconstruction showed that the regions associated with vision took up nearly one-third of the brain. Other well-developed areas involved hearing and muscle coordination. The skull scan also revealed the structure of the inner ear. The structure more closely resembles that of modern birds than the inner ear of reptiles. These characteristics taken together suggest that *Archaeopteryx* had the keen sense of hearing, balance, spatial perception and coordination needed to fly. *Archaeopteryx* had a cerebrum-to-brain-volume ratio 78% of the way to modern birds from the condition of non-coelurosaurian dinosaurs like *Carcharodontosaurus* or *Allosaurus*. Those dinosaurs had a crocodile-like anatomy of the brain and inner ear.

Archaeopteryx continues to play an important part in scientific debates about the origin and evolution of birds. Some scientists see it as a semi-arboreal climbing animal, following the idea that birds evolved from tree-dwelling gliders (the "trees down" hypothesis for the evolution of flight proposed by O.C. Marsh). Other scientists see *Archaeopteryx* as running quickly along the ground, supporting the idea that birds evolved flight by running (the "ground up" hypothesis proposed by Samuel Wendell Williston). Still others suggest that *Archaeopteryx* might have been at home both in the trees and on the ground, like modern crows, and this latter view is what today is considered best-supported by morphological characters. Altogether, it appears that the species was not particularly specialized for running on the ground or for perching. A scenario outlined by Elżanowski in 2002 suggested that *Archaeopteryx* used its wings mainly to escape predators by glides punctuated with shallow downstrokes to reach successively higher perches, and alternatively to cover longer distances by (mainly) gliding down from cliffs or treetops.

Growth



Growth trends compared with other dinosaurs and birds

A histological study by Erickson, Norell, Zhongue and others in 2009 showed that *Archaeopteryx* grew relatively slowly relative to modern birds, based on growth lines found in slices of *Archaeopteryx* bones. According to their study, all known skeletons known of *Archaeopteryx* came from juvenile specimens. They estimated that *Archaeopteryx* reached adult size in about 970 days (about 2 years and 8 months), and weighed between 0.8 - 1 kilogram. The study also found that the birds *Jeholornis* and *Sapeornis* grew slowly, as did the dromaeosaurid *Mahakala*. The birds *Confuciusornis* and *Ichthyornis*, however, grew very quickly, following a growth trend similar to that of modern birds. One of the few modern birds which exhibit slow growth is the flightless kiwi, and the authors speculated that *Archaeopteryx* and the kiwi had similar metabolisms.

Paleoecology

The richness and diversity of the Solnhofen limestones in which all specimens of *Archaeopteryx* have been found have shed light on an ancient Jurassic Bavaria strikingly different from the present day. The latitude was similar to Florida, though the climate was likely to have been drier, as evidenced by fossils of plants with adaptations for arid conditions and lack of terrestrial sediments characteristic of rivers. Evidence of plants, though scarce, include cycads and conifers while animals found include a large number of insects, small lizards, pterosaurs and *Compsognathus*.

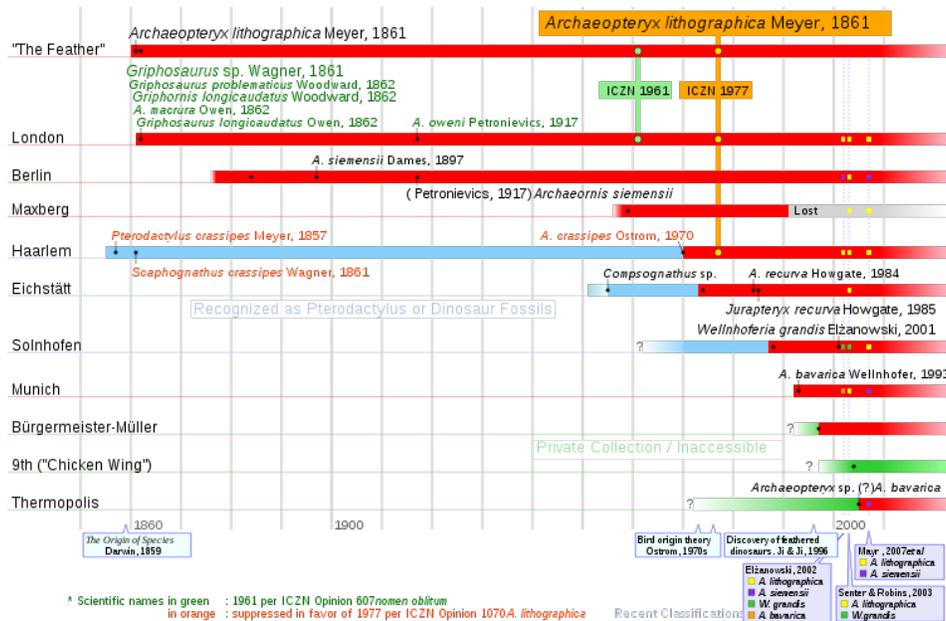
The excellent preservation of *Archaeopteryx* fossils and other terrestrial fossils found at Solnhofen indicates that they did not travel far before becoming preserved. The *Archaeopteryx* specimens found are likely therefore to have lived on the low islands surrounding the Solnhofen lagoon rather than been corpses that drifted in from farther away. *Archaeopteryx* skeletons are considerably less numerous in the deposits of Solnhofen than those of pterosaurs, of which seven genera have been found. The pterosaurs included such as *Rhamphorhynchus*, the group which dominated the niche

currently occupied by seabirds, and which became extinct at the end of the Jurassic. The pterosaurs, which also included *Pterodactylus*, were common enough that it is unlikely that the specimens found are vagrants from the larger islands 50 km (31 miles) to the north.

The islands that surrounded the Solnhofen lagoon were low lying, semi-arid and sub-tropical with a long dry season and little rain. The closest modern analogue for the Solnhofen conditions is said to be Orca Basin in the northern Gulf of Mexico, though that is much deeper than the Solnhofen lagoons. The flora of these islands was adapted to these dry conditions and consisted mostly of low (3 m [10 ft]) shrubs. Contrary to reconstructions of *Archaeopteryx* climbing large trees, these seem to have been mostly absent from the islands; few trunks have been found in the sediments and fossilized tree pollen is also absent.

The lifestyle of *Archaeopteryx* is difficult to reconstruct and there are several theories regarding it. Some researchers suggest that it was primarily adapted to life on the ground, while other researchers suggest that it was principally arboreal. The absence of trees does not preclude *Archaeopteryx* from an arboreal lifestyle; several species of extant bird live exclusively in low shrubs. Various aspects of the morphology of *Archaeopteryx* point to either an arboreal or ground existence, the length of its legs, the elongation in its feet; and some authorities consider it likely to have been a generalist capable of feeding in both shrubs, open ground and even alongside the shores of the lagoon. It most likely hunted small prey, seizing it with its jaws if it was small enough or with its claws if it was larger.

History of discovery



Timeline of *Archaeopteryx* discoveries.

Over the years, ten body fossil specimens of *Archaeopteryx* and a feather that may belong to it have been found. All of the fossils come from the limestone deposits, quarried for centuries, near Solnhofen, Germany.



The single feather

The initial discovery, a single feather, was unearthed in 1860 and described a year later by Christian Erich Hermann von Meyer. It is currently located at the Humboldt Museum für Naturkunde in Berlin. This is generally assigned to *Archaeopteryx* and was the initial holotype, but whether it actually is a feather of this species or another, as yet

undiscovered, proto-bird is unknown. There are some indications it is indeed not from the same animal as most of the skeletons (the "typical" *A. lithographica*).

Soon after, the first skeleton, known as the **London Specimen** (BMNH 37001), was unearthed in 1861 near Langenltheim, Germany and given to a local physician Karl Häberlein in return for medical services. He then sold it to the Natural History Museum in London, where it remains. Missing most of its head and neck, it was described in 1863 by Richard Owen as *Archaeopteryx macrura*, who assumed it did not belong to the same species as the feather. In the subsequent 4th edition of his *On the Origin of Species*, Charles Darwin described how some authors had maintained "that the whole class of birds came suddenly into existence during the eocene period; but now we know, on the authority of Professor Owen, that a bird certainly lived during the deposition of the upper greensand; and still more recently, that strange bird, the Archeopteryx, with a long lizard-like tail, bearing a pair of feathers on each joint, and with its wings furnished with two free claws, has been discovered in the oolitic slates of Solnhofen. Hardly any recent discovery shows more forcibly than this how little we as yet know of the former inhabitants of the world."



Replica of the London *Archaeopteryx*.

The Greek term "pteryx" (πτερυξ) primarily means "wing", but can also designate merely "feather". Von Meyer suggested this in his description. At first he referred to a single feather which appeared like a modern bird's remex (wing feather), but he had heard of and been shown a rough sketch of the London specimen, to which he referred as a "*Skelet eines mit Federn bedeckten Thiers*" ("skeleton of an animal covered in feathers"). In German, this ambiguity is resolved by the term *Schwinge* which does not necessarily mean a wing used for flying. *Urschwinge* was the favored translation of *Archaeopteryx* among German scholars in the late 19th century. In English, "ancient pinion" offers a rough approximation.

Since then ten specimens have been recovered:

The **Berlin Specimen** (HMN 1880) was discovered in 1876 or 1877 on the Blumenberg near Eichstätt, Germany, by Jakob Niemeyer. He exchanged this precious fossil for a cow, with Johann Dörr. Placed on sale in 1881, with potential buyers including O.C. Marsh of Yale University's Peabody Museum, it was bought by the Humboldt Museum für Naturkunde, where it is now displayed. The transaction was financed by Ernst Werner von Siemens, founder of the famous company that bears his name. Described in 1884 by Wilhelm Dames, it is the most complete specimen, and the first with a complete head. Once classified as a new species, *A. siemensii*, a recent evaluation supports the *A. siemensii* species definition.



Cast of the Maxberg Specimen

Composed of a torso, the **Maxberg Specimen** (S5) was discovered in 1956 or 1958 near Langenthal and described in 1959 by Heller. It is currently missing, though it was once exhibited at the Maxberg Museum in Solnhofen. It belonged to Eduard Opitsch, who loaned it to the museum. After his death in 1991, the specimen was discovered to be missing and may have been stolen or sold. The specimen is missing its head and tail, although the rest of the skeleton is mostly intact.

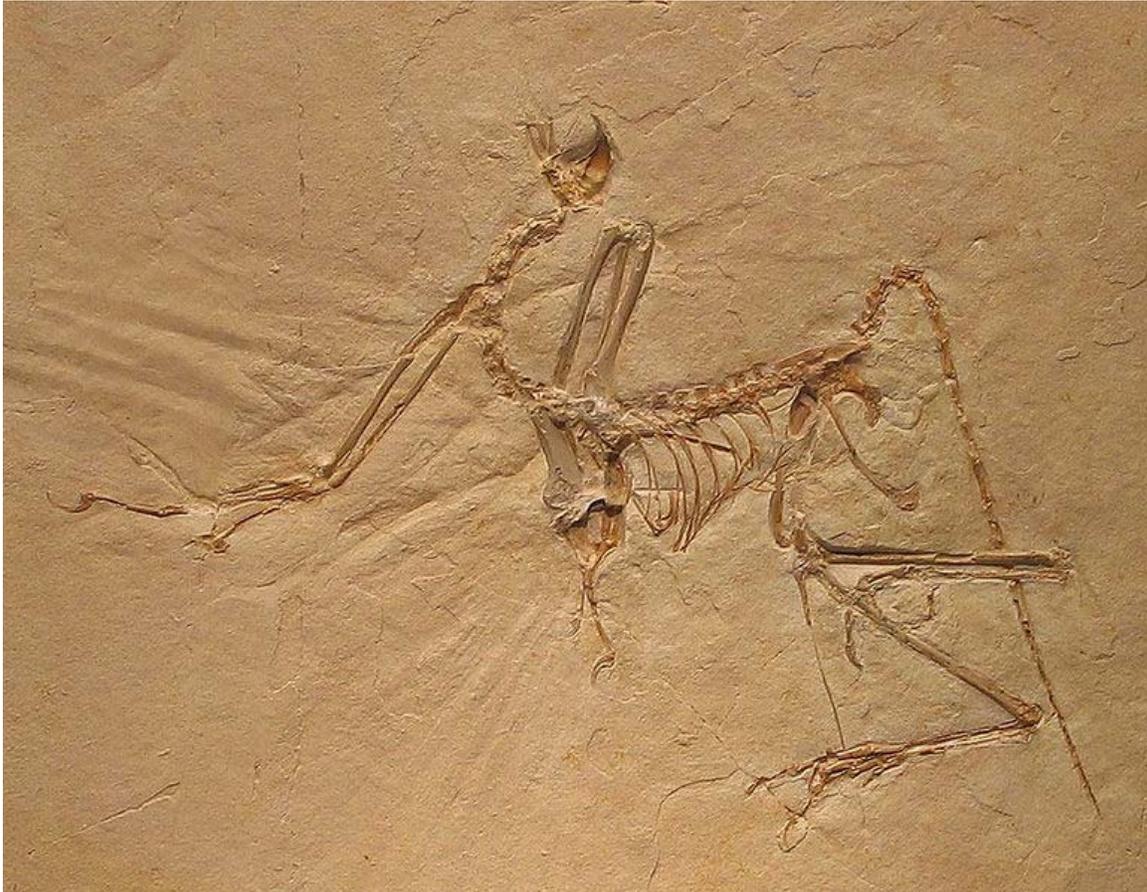


Slab of the Haarlem Specimen

The **Haarlem Specimen** (TM 6428, also known as the *Teyler Specimen*) was discovered in 1855 near Riedenburg, Germany and described as a *Pterodactylus crassipes* in 1875 by von Meyer. It was reclassified in 1970 by John Ostrom and is currently located at the Teylers Museum in Haarlem, the Netherlands. It was the very first specimen, despite the classification error. It is also one of the least complete specimens, consisting mostly of limb bones and isolated cervical vertebrae and ribs.

The **Eichstätt Specimen** (JM 2257) was discovered in 1951 or 1955 near Workerszell, Germany and described by Peter Wellnhofer in 1974. Currently located at the Jura Museum in Eichstätt, Germany, it is the smallest specimen and has the second best head. It is possibly a separate genus (*Jurapteryx recurva*) or species (*A. recurva*).

The **Solnhofen Specimen** (BSP 1999) was discovered in the 1960s near Eichstätt, Germany and described in 1988 by Wellnhofer. Currently located at the Bürgermeister-Müller-Museum in Solnhofen, it was originally classified as *Compsognathus* by an amateur collector. It is the largest specimen known and may belong to a separate genus and species, *Wellnhoferia grandis*. It is missing only portions of the neck, tail, backbone, and head.



The Munich Specimen

The **Munich Specimen** (S6, formerly known as the *Solnhofen-Aktien-Verein Specimen*) was discovered in 1991 near Langenaltheim and described in 1993 by Wellnhofer. It is currently located at the Paläontologisches Museum München in Munich. What was initially believed to be a bony sternum turned out to be part of the coracoid, but a cartilaginous sternum may have been present. Only the front of its face is missing. It may be a new species, *A. bavarica*.



Daiting Specimen

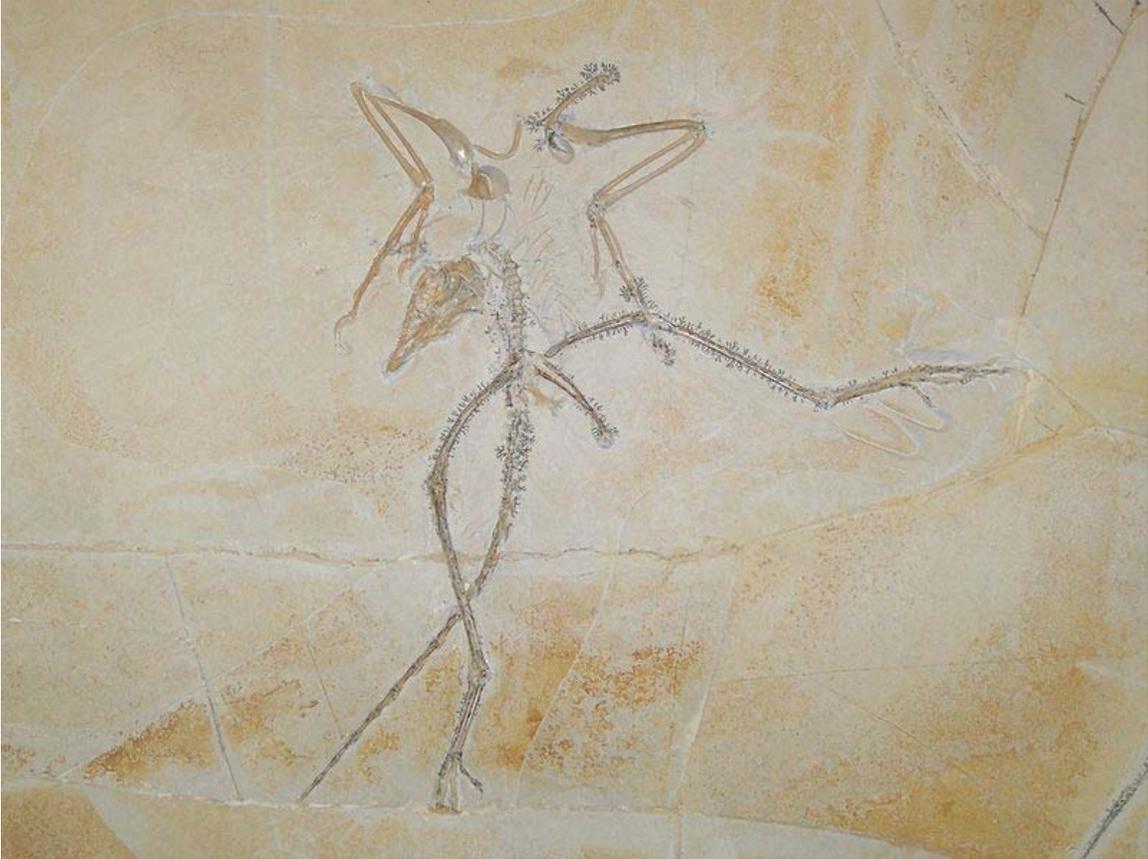
An eighth, fragmentary specimen was discovered in the late 1980s, not in Solnhofen limestone, but in somewhat younger sediments at Daiting, Suevia. It is therefore known as the **Daiting Specimen**, and has been known since 1996 only from a cast, briefly shown at the *Naturkundemuseum* in Bamberg. Long having been missing and therefore dubbed the 'Phantom', it was purchased by palaeontologist Raimund Albertsdörfer in 2009. It was on display for the first time with six other original fossils of *Archaeopteryx* at the *Munich Mineral Show* in October 2009. A first, quick look by scientists indicate that this specimen might represent a new species of *Archaeopteryx*. It was found in a limestone bed that was a few hundred thousand years younger than the other finds.



Bürgermeister-Müller ("chicken wing") Specimen

Another fragmentary fossil was found in 2000. It is in private possession and on loan to the Bürgermeister-Müller Museum in Solenhofen, so it is called the **Bürgermeister-Müller Specimen**. As the fragment represents the remains of a single wing of *Archaeopteryx*, the popular name of this fossil is "chicken wing".

Long in a private collection, the **Thermopolis Specimen** (WDC CSG 100) was discovered in Germany and described in 2005 by Mayr, Pohl, and Peters. Donated to the Wyoming Dinosaur Center in Thermopolis, Wyoming, it has the best-preserved head and feet; most of the neck and the lower jaw have not been preserved. The "Thermopolis" specimen was described in the December 2, 2005 *Science* journal article as "A well-preserved *Archaeopteryx* specimen with theropod features"; it shows that the *Archaeopteryx* lacked a reversed toe—a universal feature of birds—limiting its ability to perch on branches and implying a terrestrial or trunk-climbing lifestyle. This has been interpreted as evidence of theropod ancestry. The specimen also has a hyperextendible second toe. "Until now, the feature was thought to belong only to the species' close relatives, the deinonychosaurs." In 1988, Gregory S. Paul claimed to have found evidence of a hyperextendible toe, but this was not verified and accepted by other scientists until the Thermopolis specimen was described.



The Thermopolis Specimen

This tenth and latest specimen was assigned to *Archaeopteryx siemensii* in 2007. The specimen itself, currently on loan to the Royal Tyrrell Museum, Drumheller, Alberta, Canada, is considered the most complete and well preserved *Archaeopteryx* remains yet.

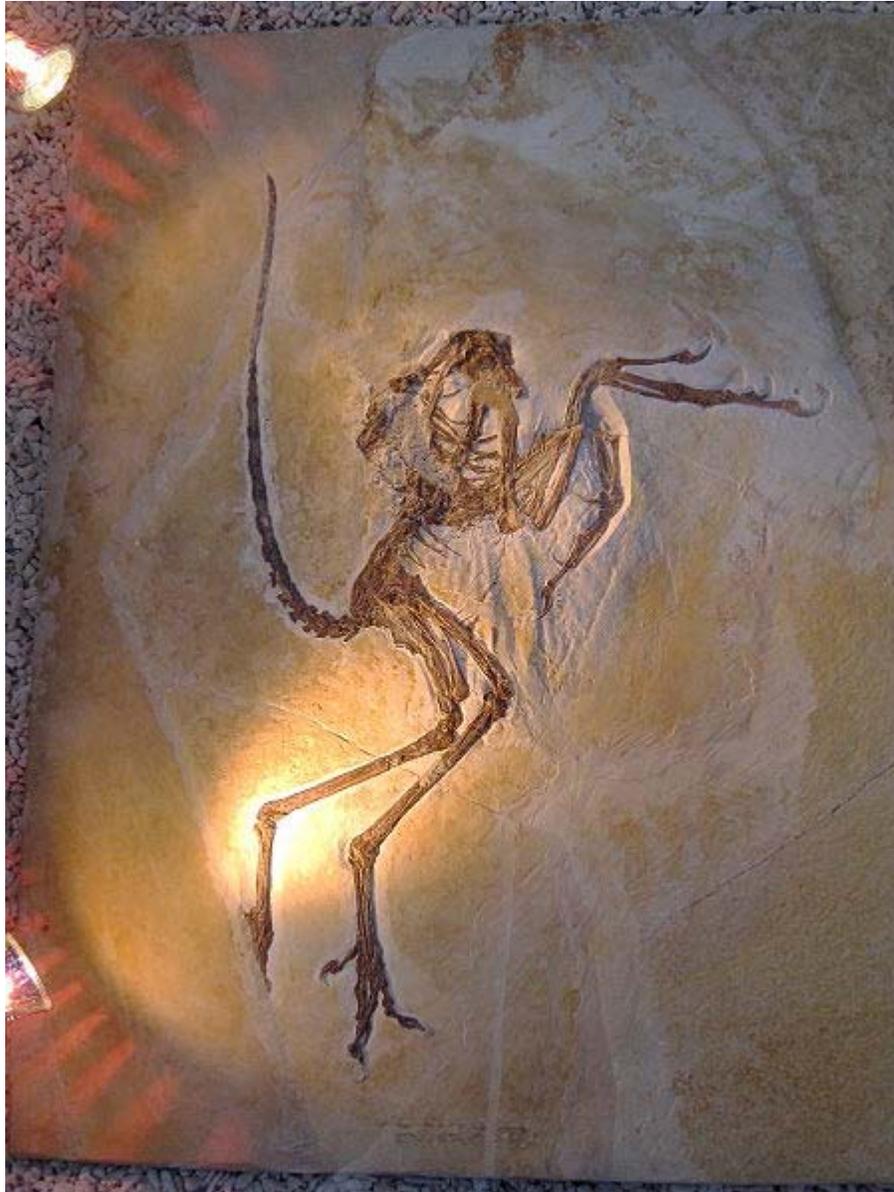
Taxonomy

Today, the fossils are usually assigned to a single species *A. lithographica*, but the taxonomic history is complicated. Dozens of names have been published for the handful of specimens, most of which are simply spelling errors (*lapsus*). Originally, the name *A. lithographica* only referred to the single feather described by von Meyer. In 1960, Swinton proposed that the name *Archaeopteryx lithographica* be officially transferred from the feather to the London specimen. The ICZN did suppress the plethora of alternative names initially proposed for the first skeleton specimens, which mainly resulted from the acrimonious dispute between von Meyer and his opponent Johann Andreas Wagner (whose *Griphosaurus problematicus*—"problematic riddle-lizard"—was a vitriolic sneer at von Meyer's *Archaeopteryx*). In addition, descriptions of *Archaeopteryx* fossils as pterosaurs before their true nature was realized were also suppressed.



Eichstätt Specimen, once considered a distinct genus, *Jurapteryx*

The relationships of the specimens are problematic. Most subsequent specimens have been given their own species at one point or another. The Berlin specimen has been designated as *Archaeornis siemensii*, the Eichstätt specimen as *Jurapteryx recurva*, the Munich specimen as *Archaeopteryx bavarica* and the Solnhofen specimen was designated as *Wellnhoferia grandis*.



The Solnhofen Specimen, by some considered as belonging to the genus *Wellnhoferia*

Recently, it has been argued that all the specimens belong to the same species. However, significant differences exist among the specimens. In particular, the Munich, Eichstätt, Solnhofen and Thermopolis specimens differ from the London, Berlin, and Haarlem specimens in being smaller or much larger, having different finger proportions, having more slender snouts, lined with forward-pointing teeth and possible presence of a sternum. These differences are as large as or larger than the differences seen today between adults of different bird species. However, it is also possible that these differences could be explained by different ages of the living birds.

Finally, it has been noted that the feather, the first specimen of *Archaeopteryx* described, does not agree well with the flight-related feathers of *Archaeopteryx*. It certainly is a

flight feather of a contemporary species, but its size and proportions indicate that it may belong to another, smaller species of feathered theropod, of which only this feather is so far known. As the feather was the original type specimen, this has created significant nomenclatorial confusion. In 2007, two sets of scientists petitioned the ICZN requesting that the London specimen be made the new holotype specimen, or neotype.

Synonyms

If two names are given, the first denotes the original describer of the "species", the second the author on whom the given name combination is based. As always in zoological nomenclature, putting an author's name in parentheses denotes that the taxon was originally described in a different genus.

- *Pterodactylus crassipes* Meyer, 1857 [suppressed in favor of *A. lithographica* 1977 per ICZN Opinion 1070]
- *Rhamphorhynchus crassipes* (Meyer, 1857) (as *Pterodactylus* (*Rhamphorhynchus*) *crassipes*) [suppressed in favor of *A. lithographica* 1977 per ICZN Opinion 1070]
- ***Archaeopteryx lithographica*** Meyer, 1861 [*nomen conservandum*]
- *Scaphognathus crassipes* (Meyer, 1857) Wagner, 1861 [suppressed in favor of *A. lithographica* 1977 per ICZN Opinion 1070]
- *Archaeopterix lithographica* Anon., 1861 [*lapsus*]
- *Griphosaurus problematicus* Wagner, 1862 [*nomen oblitum* 1961 per ICZN Opinion 607]
- *Griphornis longicaudatus* Woodward, 1862 [*nomen oblitum* 1961 per ICZN Opinion 607]
- *Griphosaurus longicaudatum* (Woodward, 1862) [*lapsus*]
- *Griphosaurus longicaudatus* (Owen, 1862) [*nomen oblitum* 1961 per ICZN Opinion 607]
- *Archaeopteryx macrura* Owen, 1862 [*nomen oblitum* 1961 per ICZN Opinion 607]
- *Archaeopterix macrura* Owen, 1862 [*lapsus*]
- *Archaeopterix macrurus* Egerton, 1862 [*lapsus*]
- *Archeopteryx macrurus* Owen, 1863 [unjustified emendation]
- *Archaeopteryx macroura* Vogt, 1879 [*lapsus*]
- *Archaeopteryx siemensii* Dames, 1897
- *Archaeopteryx siemensi* Dames, 1897 [*lapsus*]
- *Archaeornis siemensii* (Dames, 1897) Petronievics, 1917
- *Archaeopteryx oweni* Petronievics, 1917 [*nomen oblitum* 1961 per ICZN Opinion 607]
- *Gryphornis longicaudatus* Lambrecht, 1933 [*lapsus*]
- *Gryphosaurus problematicus* Lambrecht, 1933 [*lapsus*]
- *Archaeopteryx macrourus* Owen, 1862 *fide* Lambrecht, 1933 [*lapsus*]
- *Archaeornis siemensi* (Dames, 1897) *fide* Lambrecht, 1933? [*lapsus*]
- *Archeopteryx macrura* Ostrom, 1970 [*lapsus*]
- *Archaeopteryx crassipes* (Meyer, 1857) Ostrom, 1972 [suppressed in favor of *A. lithographica* 1977 per ICZN Opinion 1070]
- *Archaeopterix lithographica* di Gregorio, 1984 [*lapsus*]
- *Archaeopteryx recurva* Howgate, 1984
- *Jurapteryx recurva* (Howgate, 1984) Howgate, 1985
- *Archaeopteryx bavarica* Wellnhofer, 1993

- *Wellnhoferia grandis* Elżanowski, 2001

The last 4 taxa may be valid genera and species.

"Archaeopteryx" vicensensis (Anon. *fide* Lambrecht, 1933) is a *nomen nudum* for what appears to be an undescribed pterosaur.

Controversies

Authenticity

Beginning in 1985, a group including astronomer Fred Hoyle and physicist Lee Spetner published a series of papers claiming that the feathers on the Berlin and London specimens of *Archaeopteryx* were forged. Their claims were repudiated by Alan J. Charig and others at the British Museum (Natural History). Most of their evidence for a forgery was based on unfamiliarity with the processes of lithification; for example, they proposed that based on the difference in texture associated with the feathers, feather impressions were applied to a thin layer of cement, without realizing that feathers themselves would have caused a textural difference. They also expressed disbelief that slabs would split so smoothly, or that one half of a slab containing fossils would have good preservation, but not the counterslab. These, though, are common properties of Solnhofen fossils because the dead animals would fall onto hardened surfaces which would form a natural plane for the future slabs to split along, leaving the bulk of the fossil on one side and little on the other. They also misinterpreted the fossils, claiming that the tail was forged as one large feather, when this is visibly not the case. In addition, they claimed that the other specimens of *Archaeopteryx* known at the time did not have feathers, which is untrue; the Maxberg and Eichstätt specimens have obvious feathers. Finally, the motives they suggested for a forgery are not strong, and contradictory; one is that Richard Owen wanted to forge evidence in support of Charles Darwin's theory of evolution, which is unlikely given Owen's views toward Darwin and his theory. The other is that Owen wanted to set a trap for Darwin, hoping the latter would support the fossils so Owen could discredit him with the forgery; this is unlikely because Owen himself wrote a detailed paper on the London specimen, so such an action would certainly backfire.

Charig *et al.* pointed to the presence of hairline cracks in the slabs running through both rock and fossil impressions, and mineral growth over the slabs that had occurred before discovery and preparation, as evidence that the feathers were original. Spetner *et al.* then attempted to show that the cracks would have naturally propagated through their postulated cement layer, but neglected to account for the fact that the cracks were old and had been filled with calcite, and thus were not able to propagate. They also attempted to show the presence of cement on the London specimen through X-ray spectroscopy, and did find something that was not rock. However, it was not cement, either, and is most probably from a fragment of silicone rubber left behind when molds were made of the specimen. Their suggestions have not been taken seriously by palaeontologists, as their evidence was largely based on misunderstandings of geology, and they never discussed the other feather-bearing specimens, which have increased in number since then. Charig

et al. reported a discoloration: a dark band between two layers of limestone – however, they say it is the product of sedimentation. It is natural for limestone to take on the color of its surroundings and most limestones are colored (if not color banded) to some degree – the darkness was attributed to such impurities. They also mention that a complete absence of air bubbles in the rock slabs is further proof that the specimen is authentic.

Archaeopteryx* and *Protoavis

In 1984, Sankar Chatterjee discovered fossils which he claimed in 1991 belonged to a fossil bird far older than *Archaeopteryx*. These fossils, believed to be around 210 to 225 million years old, have been assigned the name *Protoavis*. The fossils are too badly preserved to allow an estimate of flying ability; although Chatterjee's reconstructions usually show feathers, many paleontologists, including Paul (2002) and Witmer (2002) have rejected the claims that *Protoavis* was an earlier bird (or, alternately, that it existed at all). The fossils were found disarticulated, and were collected from different locations. Because the fossils are in poor condition, *Archaeopteryx* remains the earliest universally recognized bird.

Phylogenetic position

Modern paleontology has consistently placed *Archaeopteryx* as the most primitive bird. It is not thought to be a true ancestor of modern birds but, rather, a close relative of that ancestor. Nonetheless, *Archaeopteryx* is so often used as a model of the true ancestral bird that it has seemed almost heretical to suggest otherwise. Several authors have done so. Lowe (1935) and Thulborn (1984) questioned whether *Archaeopteryx* truly was the first bird. They suggested that *Archaeopteryx* was a dinosaur that was no more closely related to birds than were other dinosaur groups. Kurzanov (1987) suggested that *Avimimus* was more likely to be the ancestor of all birds than *Archaeopteryx*. Barsbold (1983) and Zweers and Van den Berge (1997) noted that many maniraptoran lineages are extremely birdlike, and suggested that different groups of birds may have descended from different dinosaur ancestors.

Chapter 5

Darwinius

Darwinius

Temporal range: Eocene, 47 Ma



Main slab of the *Darwinius masillae* holotype fossil
(specimen PMO 214.214)

Scientific classification

Kingdom: Animalia

Phylum: Chordata

Class: Mammalia
Order: Primates
Family: Notharctidae
Subfamily: Cercamoniinae
Genus: *Darwinius*
Franzen *et al.*, 2009
Species: *D. masillae*

Binomial name

Darwinius masillae
Franzen *et al.*, 2009

Darwinius is a genus of Adapiformes, a group of basal primates from the Eocene epoch. Its only known species is *Darwinius masillae*, dated to 47 million years ago (Lutetian stage) based on dating of the fossil site.

The only known fossil, dubbed **Ida**, was discovered in 1983 at the Messel pit. The fossil, divided into a slab and partial counterslab after the amateur excavation and sold separately, was not reassembled until 2007. The fossil is of a juvenile female, approximately 58 cm (23 in) overall length, with the head and body length excluding the tail being about 24 cm (9.4 in). It is estimated that Ida died at about 80–85% of her projected adult body and limb length.

The genus *Darwinius* was named in commemoration of the bicentenary of the birth of Charles Darwin, and the species name *masillae* honors Messel where the specimen was found. The creature appeared superficially similar to a modern lemur.

The authors of the paper describing *Darwinius* classified it as a member of the primate family Notharctidae, subfamily Cercamoniinae, suggesting that it has the status of a significant transitional form (a "link") between the prosimian and simian ("anthropoid") primate lineages. Others have disagreed with this placement.

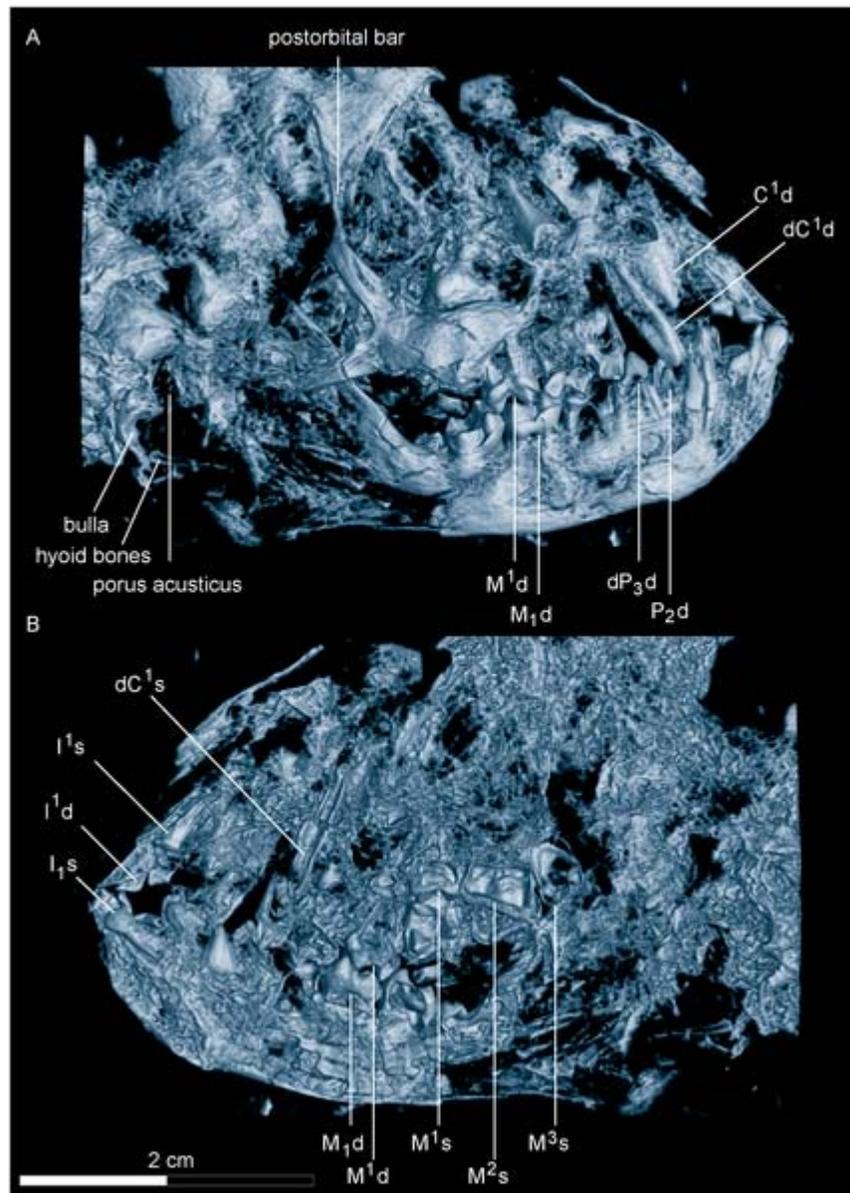
Concerns have been raised about the claims made about the fossil's relative importance, and the publicising of the fossil before adequate information was available for scrutiny by the academic community.

Taxonomy

Franzen *et al.* (2009) place the *Darwinius* genus in the Cercamoniinae subfamily of the Notharctidae family within the extinct Adapiformes suborder of early primates.

Darwinius masillae is the third primate species to be discovered at the Messel locality that belongs to the cercamoniine adapiforms, in addition to *Europolemur koenigswaldi* and *Europolemur kelleri*. *Darwinius masillae* is similar but not directly related to *Godinotia neglecta* from Geiseltal.

The adapiforms are early primates which are known only from the fossil record, and it is unclear whether they form a suborder proper, or a paraphyletic grouping. They are usually grouped under Strepsirrhini—including Lemurs, Aye-ayes and Lorisiformes—and as such would not be ancestral to Haplorrhini which includes tarsiers and simians. Simians are usually called anthropoids, and while this name can be confusing, the paper uses the term anthropoids, as does associated publicity material. Simians (anthropoids) include monkeys and apes, which in turn includes humans.



CT image of the skull of *Darwinius*

Franzen et al. in their 2009 paper place *Darwinius* in the "Adapoidea group of early primates representative of early haplorhine diversification". This means that according to these authors, the adapiforms would not be entirely within the Strepsirrhini lineage as

hitherto assumed but would qualify as a transitional fossil (a "missing link") between Strepsirrhini and Haplorrhini, and so could be ancestral to humans. They also suggest that tarsiers have been misplaced in the Haplorrhini, and should be considered Strepsirrhini. To support this view, they show that as many as 6 morphological traits found in "Darwinius" are derived characters present only in the Haplorrhini lineage but absent in the Strepsirrhini lineage, which they interpret as synapomorphies. These include, among others, a cranium with a short rostrum, deep mandibular ramus, loss of all grooming claws. They note "that *Darwinius masillae*, and adapoids contemporary with early tarsioids, could represent a stem group from which later anthropoid primates evolved, but we are not advocating this here, nor do we consider either *Darwinius* or adapoids to be anthropoids."

Concerns over cladistic analysis

Paleontologists have expressed concern that the cladistic analysis compared only 30 traits, when standard practice is to analyze 200 to 400 traits and to include fossils such as anthropoids from Egypt and the primate genus *Eosimias* which were not included in the analysis. This contrasts with the motive openly stated by the authors, which was to list 30 anatomical and morphological characteristics "commonly used" to distinguish extant strepsirrhine and haplorrhine primates. Paleontologist Richard Kay of Duke University thought the data could have been cherry-picked, and paleontologist Callum Ross of the University of Chicago considered the claim that *Darwinius* should be classified as haplorrhine was "unsupportable in light of modern methods of classification." The opinion of Chris Beard, curator of vertebrate paleontology at the Carnegie Museum of Natural History, was that *Darwinius* was not a "missing link" between anthropoids and more primitive primates, but that further study of this remarkably complete specimen would be very informative and could reveal relationships amongst "the earliest and least human-like of all known primates, the Eocene adapiforms." In an interview published on 27 May, Jørn Hurum stated that he had an open mind about the possibility that the fossil might turn out to be a lemur, and that a paper on systematics to be published within about a year would mainly focus on the partial counterslab containing the inner ear and the foot bones.

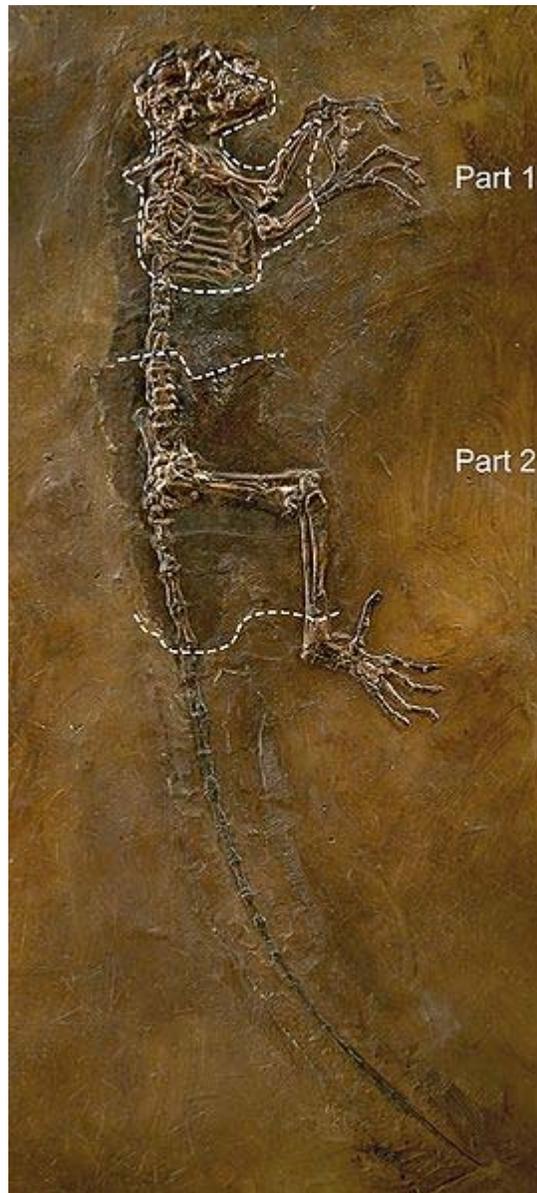
Most experts hold that the higher primates (simians) evolved from Tarsiidae, branching off the Strepsirrhini before the appearance of the Adapiformes. A smaller group agrees with Franzen et al. that the higher primates descend from Adapiformes (Adapoidea). The view of paleontologist Tim White is that *Darwinius* is unlikely to end the argument.

Philip D. Gingerich states that the seven superfamilies of Primates are commonly associated in the higher taxonomic groupings of suborders Anthropeidea and Prosimii as an alternative to Haplorhini and Strepsirrhini, depending on the position of Adapoidea and Tarsioidea. He puts forward a phylogeny in which the higher primates evolved from *Darwinius*, which he groups with other Adapoidea. He shows the Adapoidea together the Tarsioidea as representing early diversification of the suborder Haplorhini, and shows the Strepsirrhini as having branched off directly from the earliest primates. The Revealing the Link website uses this taxonomic grouping, and states that *Darwinii* is from an early

group of primates, just prior to diversification into the anthropoids (monkeys, apes and humans) and the prosimians (lemurs, lorises and tarsiers).

Erik Seiffert and colleagues at Stony Brook University argue that *Darwinius* is on the branch towards the Strepsirrhini, and is not a 'missing link' in the evolution of the Anthroidea. A phylogenetic analysis of 360 morphological characters in 117 extinct and modern primates places *Darwinius* in a now-extinct group of strepsirrhines, along with a newly discovered 37-million-year-old Egyptian primate, *Afradapis*. Seiffert believes that characteristics that appeared to show a relationship to haplorrhines are due to convergent evolution, and has said that "the PR hype surrounding the *Darwinius* description was very confusing."

Type specimen



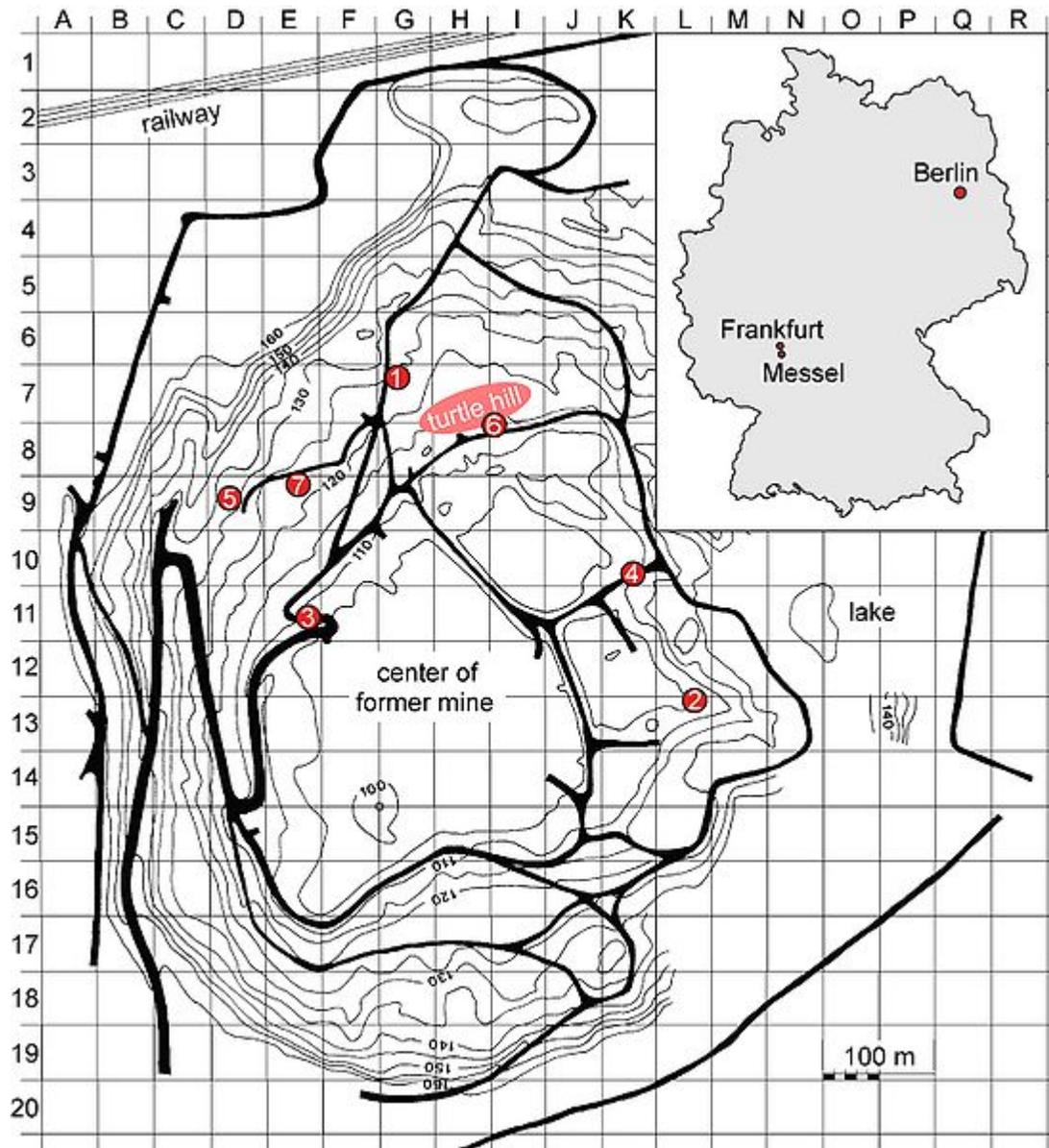
Counter-slab of the *Darwinius masillae* holotype fossil (specimen WDC-MG-210 reversed for comparison). Parts 1 and 2 (enclosed in dashed lines) are genuine; remainder of plate B was fabricated during preparation

The type specimen is a 95%-complete fossil, missing only its left rear leg. It has been named Ida after the daughter of Jørn Hurum, the Norwegian vertebrate paleontologist from the Natural History Museum, University of Oslo, who secured one section of the fossil from an anonymous owner, and led the research. In addition to the bones, remains of Ida's soft tissue and fur outline are present, along with remnants of her last meal of fruit and leaves. The animal is about 58 cm (23 in) from nose to tail, or roughly the size of a small, long-tailed cat.

The lemur-like skeleton of the fossil features primate characteristics of grasping hands with opposable thumbs and nails instead of claws. These would have provided a "precision grip" which, for Ida, was useful for climbing and gathering fruit. Ida also has flexible arms and relatively short limbs. The fossil is missing two anatomical features found in modern lemurs: a grooming claw on the foot and a fused row of teeth, a toothcomb, in the bottom jaw.

Digital reconstructions of Ida's teeth reveal that she has unerupted molars in her jaw, indicating by comparison with modern squirrel monkeys that she was 9–10 months old, and would have reached adulthood at 36 months. The shape of Ida's teeth provides clues as to her diet; jagged molars would have allowed her to slice food, suggesting that she was a leaf and seed eater. This is confirmed by the remarkable preservation of her gut content. Furthermore the lack of a baculum (penis bone) found in all lower primates means that the fossil was from a female. X-rays performed on Ida revealed that her right wrist was healing from a fracture, which may have contributed to her death. The scientists speculate whether she was overcome by carbon dioxide fumes while drinking from the Messel lake. Hampered by her broken wrist, she slipped into unconsciousness, was washed into the lake and sank to the bottom, where unique fossilisation conditions preserved her for 47 million years.

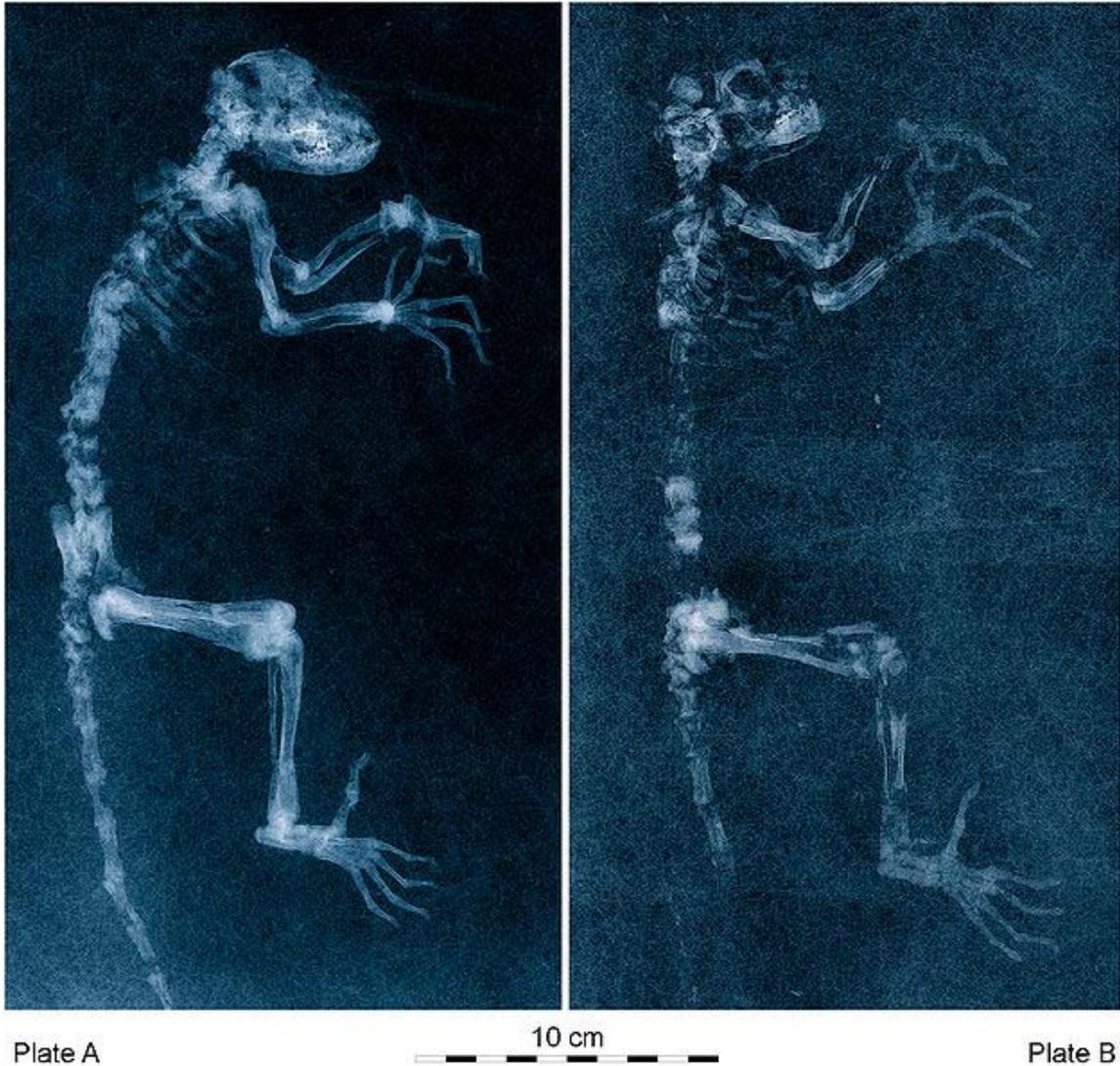
Discovery and acquisition



Map showing where *Darwinius* (6) and other primates have been found in the Messel pit

The events regarding the original unearthing of the fossil are not clear, though some facts are known. It was found at the Messel pit in 1983, a disused shale quarry noted for its astonishing fossil preservation, near the village of Messel, about 35 km (22 mi) southeast of Frankfurt am Main in Germany. The fossil came as a slab and partial counter slab, and was expertly prepared by encasing each slab in resin using the transfer technique necessary to conserve Messel fossils. At some point the slab and counter slab went separate ways. The counter slab was incorporated in a composite of fabricated parts to represent a complete specimen, and arrived at a private Wyoming museum in 1991. Analysis by Jens Franzen of the Natural History Museum of Basel, Switzerland revealed

the mixed actual and faked nature of this slab. A comparison of the two slabs indicates that the forger had access to the whole fossil.



Radiographs of the *Darwinius* holotype fossil, revealing the fabricated parts of the counter-slab

The primary slab remained in Germany, in the possession of a private collector who kept it secret for twenty years before deciding to sell it anonymously via a German fossil dealer. Two German museums turned it down as too expensive, then a year later at the Hamburg Fossil and Mineral Fair in December 2006 the dealer asked Norwegian vertebrate palaeontologist Jørn Hurum, who had done some previous deals, to discuss something privately. The dealer showed Hurum three high resolution colour photographs of the fossil, and told him that the asking price was \$1 million. Hurum knew that it was a primate, and according to Tudge's book "was fast concluding that the specimen he was looking at could be one of the holy grails of science — the 'missing link' from the crucial

time period." He asked for time until after Christmas to organise funding to pay for the specimen and ensure that it had been legally collected, had an export permit and would be legitimately available for study. His first choice was the Natural History Museum of Oslo, but it was beyond their means and he began to think of other museums with sponsors available. He persuaded the Oslo museum to make half the funding available, with the remainder to be paid only after X-ray scans proved conclusively that it was not a fake, a process which took several months. He put together a team including leading German experts on the Messel fossils, ensuring international ownership.

After its acquisition it was studied in secret for two years by a team of scientists led by Hurum, who was joined by primate evolution expert Professor Philip Gingerich of the University of Michigan, and palaeontologists Jens Franzen who had studied the counter slab and Jörg Habersetzer of the Senckenberg Museum's Research Institute.

Publication

While studies were in progress, negotiations were put in place for a book and with various broadcasters for documentary programs, all of whom agreed to keep the project secret. A deal went through in the summer of 2008 with The History Channel which has been reported as paying more for this than any other documentary. The team decided to publish their findings online in *PLoS ONE*, an open access journal of the Public Library of Science. The paper for publication was received by *PLoS ONE* on March 19, 2009, and accepted on May 12, 2009.

On May 10, 2009, the *Daily Mail* published reports that the BBC had made a documentary revealing the discovery of what might be a vital 'missing link' in human evolution, giving an outline of the study and its intended publication date as well as a brief statement from Gingerich. On 15 May the *Wall Street Journal* carried a report with interviews with Gingerich and with Tim White, who cautioned that "Lemur advocates will be delighted, but tarsier advocates will be underwhelmed". At about the same time a press release headed "World Renowned Scientists Reveal a Revolutionary Scientific Find That Will Change Everything" announced that the find was "lauded as the most significant scientific discovery of recent times."

On May 19, 2009, the team revealed their findings to the world at a press conference, simultaneously with online publication of the paper in *PLoS ONE* (for naming purposes, the paper was officially published in print on May 21, 2009). The paper included a statement that the authors were not advocating the possibility that the species could be ancestral to later anthropoid primates; Professor John Fleagle, of Stony Brook University in New York state, asserted that he was one of the anonymous scientific reviewers of the paper, and that he had explicitly requested before publication that the authors tone down their original claims that the fossil was on the human evolutionary line. At the press conference, the fossil was described as the "missing link" in human evolution. Hurum said that "This fossil rewrites our understanding of the evolution of primates... It will probably be pictured in all the textbooks for the next 100 years," and compared its importance to the Mona Lisa. He also said that *Darwinius* was "the closest thing we can

get to a direct ancestor" and that finding it was "a dream come true". Team member Jens Franzen said the state of preservation was "like the Eighth Wonder of the World", with information "palaeontologists can normally only dream of", but while he said it bore "a close resemblance to ourselves" in some aspects, other features indicated that it was not a direct ancestor.

Independent experts were quick to question the claims. Henry Gee, a senior editor at Nature, said the term "missing link" was misleading and that the scientific community would need to evaluate its significance, which was unlikely to match that of *Homo floresiensis* or feathered dinosaurs. Chris Beard, curator of the Carnegie Museum of Natural History, said he "would be absolutely dumbfounded if it turns out to be a potential ancestor to humans."

Publicity and media coverage



Life restoration of *Darwinius*

Having previously experienced how the blogosphere had picked up on his work, and seen Chinese dinosaur finds the object of bad early descriptions from blogging, Jørn Hurum decided to orchestrate launch of the fossil in a combined scientific and public event. Atlantic Productions, which had cooperated with Hurum on a program on the Predator X, a giant pliosaur from Svalbard, was brought in on the project in order to "take story straight to the masses in a way that would appeal to the average person, especially kids". The press conference and paper on the fossil was accompanied by the launch of a website, the publication of a book which had already been distributed to bookstores, *The Link: Uncovering Our Earliest Ancestor* by Colin Tudge, and the announcement of a documentary (*Uncovering Our Earliest Ancestor: The Link*), made by Atlantic

Productions in the UK, directed by Tim Walker and produced by Lucie Ridout, to be screened six days later on the History Channel (US), BBC One (UK), and various stations in Germany and Norway. The New York *Daily News* noted that "The unveiling of the fossil came as part of an orchestrated publicity campaign unusual for scientific discoveries".

One of the paper's co-authors, paleontologist Philip D. Gingerich, expressed dissatisfaction with the media campaign, telling *The Wall Street Journal* that they had chosen to publish in *PLoS ONE* as "There was a TV company involved and time pressure" and they had been pushed to finish the study. "It's not how I like to do science", Gingerich concluded. In an interview, Jørn Hurum said that *PLoS ONE* had been chosen as it was open access and the research had been funded by Norwegian taxpayers who would benefit from free access, it did not restrict the length of manuscript or number of illustrations, and "*PLoS ONE* is the quickest way to publish a large work in the world!"

At the time its discovery was announced in the scientific and the popular press, the fossil was characterized as the "most complete fossil primate ever discovered"; Sir David Attenborough has described it as "extraordinary". Google commemorated the unveiling with a themed logo on May 20, 2009. During a ceremony at the American Museum of Natural History Hurum said that "This specimen is like finding the Lost Ark for archeologists" and "It is the scientific equivalent of the Holy Grail. This fossil will probably be the one that will be pictured in all textbooks for the next 100 years." Regarding the publicity, Matt Cartmill an anthropologist from Duke University said "The P.R. campaign on this fossil is I think more of a story than the fossil itself".

Independent experts have raised concern about publicity exaggerating the importance of the find before information was available for scrutiny. Chris Beard, curator of the Carnegie Museum of Natural History, was "awestruck" by the publicity machine but concerned that if the hype was exaggerated, it could damage the popularisation of science if the creature was not all that it was hyped up to be. Paleoanthropologist Elwyn Simons of Duke University stated that it is a wonderful specimen but most of the information had been previously known, and paleoanthropologist Peter Brown of the University of New England said that the paper had insufficient evidence that *Darwinius* was ancestral to the simians. Others have also criticized claims that the fossil represents the "missing link in human evolution", arguing that there is no such thing unless evolution is visualized as a chain as there are an enormous number of missing branches, and that while the fossil is a primate, there is no evidence to suggest that its species is a direct ancestor of humans. ScienceBlogger Brian Switek questioned the sensationalist coverage of claims of ancestral relationships made before a full cladistic analysis, and in a column in *The Times* he stated that a unique opportunity to communicate science had been lost, with press releases forestalling the necessary discovery and debate which should now proceed.

Hurum considered that the risk of buying the fossil had paid off, and said that "You need an icon or two in a museum to drag people in, this is our Mona Lisa and it will be our Mona Lisa for the next 100 years." He has been described as "a modern-era, media-savvy scientist with the right amounts of showmanship, populist sensibility, and disregard for

the normal avenues of scientific prestige required to pull this off". The debut in "an astonishingly slick, multi-component media package" required exceptional coordination between networks, museums, producers and scientists while maintaining a level of secrecy which is hard to attain in modern circumstances. In interviews published on 27 May, Hurum stated that it was good that they had got the message out that primates were rooted deep in time, but that some of the slogans were too much and the publicity got completely out of control. He disclosed that he paid nearly \$750,000 (£465,000) for the specimen, but felt it was worthwhile to make the fossil available for scientific investigation instead of it being bought by a private collector and hidden away. Others including Chris Beard were concerned that the price and publicity could lead to profiteering by amateur collectors, and make acquisition of specimens for research purposes more difficult.

Chapter 6

Darwinopterus

Darwinopterus

Temporal range: Middle Jurassic, 160 Ma



D. modularis fossil

Scientific classification [e]

Kingdom: Animalia
Phylum: Chordata
Class: Reptilia
Order: †Pterosauria
Family: †Wukongopteridae
Genus: †*Darwinopterus*
Lü *et al.*, 2010

Species

- *D. modularis* Lü *et al.*, 2010 (type)
- *D. linglongtaensis* Wang *et al.*, 2010

Darwinopterus (meaning "Darwin's wing") is a genus of pterosaur, discovered in China and named after biologist Charles Darwin. Between 30 and 40 fossil specimens have been identified, all collected from the Tiaojishan Formation, which dates to the middle Jurassic period. The type species, *D. modularis*, was described in February of 2010. *D. modularis* was the first known pterosaur to display features of both long-tailed (rhamphorhynchoid) and short-tailed (pterodactyloid) pterosaurs, and was described as a transitional fossil between the two groups. A second species, *D. linglongtaensis*, was described from the same fossil beds in December of 2010.

Description



Restoration of a crested *D. modularis*

Darwinopterus, like its closest relatives, is characterized by its unique combination of basal and derived pterosaurian features. While it had a long tail and other features characteristic of the "rhamphorhynchoids", it also had distinct pterodactyloid features, such as long vertebrae in the neck and a single skull opening in front of the eyes, the nasoantorbital fenestra (in most rhamphorhynchoids, the antorbital fenestra and the nasal opening are separate).

Darwinopterus is distinguished from its close relatives by the greater relative length of the back portion of the skull compared to its jaws, thin nasal bone, and elongated hip bone (ilium). Unlike other wukongopterids, the head crest found in males was supported by a thin bony extension of the skull, with a serrated top edge. The serrations probably helped anchor an even larger keratin extension.

Specimens of *Darwinopterus* have been divided into two distinct species. The first to be named, *D. modularis*, had an especially elongated back end to the skull, and widely-spaced, "spike-like" teeth. *D. linglongtaensis*, on the other hand, had a shorter and taller skull and shorter, cone-shaped teeth.

Biology

Because *Darwinopterus* is known from numerous well-preserved specimens including an egg, scientists have been able to deduce various aspects of its biology, including growth patterns and life history, reproduction, and possible variation between sexes.

Sexual variation

Darwinopterus specimens have been reported to show several differences between males and females. Distinct *dimorphism* (variation that can separate specimens into two distinct categories) can be seen across the large number of known specimens. In one specimen category, individuals have small, narrow hips and often large crests on their skulls. The other specimen type has larger, broader hips and often have small crests or no crests at all. However, while these were thought to represent different sexes, no direct evidence was found at first to determine which was male and which was female. The first specimen in which sex could be confidently identified was specimen M8802 in the collections of the Zhejiang Museum of Natural History, nicknamed "Mrs T" (short for "Mrs Pterodactyl"), described by Lü Junchang and colleagues in January 2011. This specimen was preserved with the impression of an egg between its thighs in close association with its pelvis. This specimen had a broad pelvis (matching the diameter of the egg) and lacked any evidence of a crest. This link to an unhatched egg, which was probably expelled from the body during decomposition, allowed scientists to identify the second, crestless type of *Darwinopterus* as the females.

Pterosaur researcher Kevin Padian, however, questioned some of the conclusions drawn about this specimen by Lü and his colleagues. Padian suggested in a 2011 interview that in other animals with elaborate display crests (such as ceratopsian dinosaurs), the size and shape of the crests change dramatically with age. He noted that the "Mrs T" specimen may simply have been a sub-adult which had not yet developed a crest (most animals are able to reproduce before they are fully grown).

Reproduction

The specimen preserved along with an egg (nicknamed "Mrs T"), described by Lü and colleagues in 2011, offers insight into the reproductive strategies of *Darwinopterus* and pterosaurs in general. Like the eggs of later pterosaurs and modern reptiles, the eggs of *Darwinopterus* had a parchment-like, soft shell. In modern birds, the eggshell is hardened with calcium, completely shielding the embryo from the outside environment. Soft-shelled eggs are permeable, and allow significant amounts of water to be absorbed into the egg during development. Eggs of this type are more vulnerable to the elements and are typically buried in soil. The eggs of *Darwinopterus* would have weighed about 6 grams (0.21 oz) when they were laid, but due to moisture intake, they may have doubled in weight by the time of hatching. The eggs were small compared to the size of the mother (the "Mrs T" specimen weighed between 110 grams (3.9 oz) and 220 grams (7.8 oz)), also more like modern reptiles than birds. David Unwin, a co-author of the paper, suggested that *Darwinopterus* probably laid many small eggs at a time and buried

them, and that juveniles could fly upon hatching, requiring little to no parental care. These results imply that reproduction in pterosaurs was more like that in modern reptiles and significantly differed from reproduction in birds.

Implications

As the name *Darwinopterus modularis* implies, the researchers who first described this genus saw it as evidence that pterodactyloid pterosaurs evolved from the more primitive "rhamphorhynchoids" via modular evolution. In other words, rather than a gradual change from one body type to the other, various major aspects of pterodactyloid anatomy arose piecemeal, producing species with distinct combinations of both primitive and advanced features.

Chapter 7

Eupodophis and Odontochelys

Eupodophis

Eupodophis
Temporal range: Late
Cretaceous, 92 Ma



Fossil of *Eupodophis descouensi*

Scientific classification

Kingdom: Animalia
Phylum: Chordata
Class: Sauropsida
Subclass: Diapsida
Order: Squamata
Suborder: Serpentes

Genus: *Eupodophis*
Rage and
Escuillié, 2000

Species

- †*E. descouensi*
Rage and Escuillié,
2000 (type)

Eupodophis is an extinct genus of snake from the Late Cretaceous period. It has two small hind legs and is considered a transitional form between Cretaceous lizards and

limbless snakes. The feature, described as vestigial, was most likely useless to *Eupodophis*. The type species *Eupodophis descouensi* was named in 2000. The specific name is dedicated to the French naturalist Didier Descouens.

The fossilized specimen from which the description of the type species was based was 85 cm (33.5 in) long and is approximately 92 million years old. It was found in Cenomanian-age limestone near the al-Nammoura village in Lebanon.

Description

Eupodophis was a marine snake that lived in the Mediterranean Tethys Ocean. It had a laterally compressed body and short, paddle-like tail. The vertebrae and ribs of *Eupodophis* are pachyostotic, or thickened, as an adaptation to a marine lifestyle. The pelvic bones are small and weakly attached to each other. Tarsal bones are present but reduced in size and form. The metatarsals and phalanges of the foot are absent.

The fossil skeleton of *Eupodophis* was analyzed using synchrotron x-rays at the European synchrotron radiation facility in Grenoble, France. The researchers determined that the hind limb on one skeleton was 0.8 inches long, with an "unmistakable" fibula, tibia and femur. One limb was visible on the surface of the fossil while the other was hidden within the limestone. The scans were compared with similar ones taken of the limbs of extant lizards including the Gila monster, Green Iguana, and several species of monitor lizard.



The hind limb of *Eupodophis*

While they are very small in comparison to limbed reptiles, the hind limbs of *Eupodophis* possess much of the same anatomy as modern lizards. This suggests that the bones of *Eupodophis* became reduced in size through a change in the rate of bone growth, not major anatomical changes. The lack of thickening at either end of the limb bones

suggests that growth had stopped occurring in the limbs at one point in the animal's lifetime. While the vertebrae and ribs of *Eupodophis* are pachyostotic and osteosclerotic (meaning that the outer and inner parts of the bone are compact), the limb bones remain light. This lightness is also seen in the bones of terrestrial lizards, suggesting that the limbs had not been part of the overall adaptation of the skeleton for an aquatic lifestyle.

Paleobiology

The loss of limbs in *Eupodophis* may have been the result of changes in Hox genes, genes that specify the development specific regions of the body. Because Hox genes are involved in determining specific features of the axial skeleton, the loss of limbs would also result in the loss of cervical (tail) vertebrae that are near them. This loss is seen in *Eupodophis* and modern snakes but not legless lizards, which may be far less common because some other factor besides Hox genes were involved in the loss of their limbs. The loss of digits on the hind limbs may be explained by a low number of cells in the limb bud during embryonic development.

The loss of forelimbs and reduction of hind limbs in *Eupodophis* was likely an adaptation for swimming. While living snakes usually employ undulatory movement for moving over land, sinuous movements are also an effective means of moving through water. Large, well-developed limbs increase drag on swimming animals, so the limbs of *Eupodophis* and other early snakes may have become vestigial to save energy and make movement more efficient.

Odontochelys

Odontochelys

Temporal range: Late Triassic,
220 Ma



Scientific classification

Kingdom: Animalia
Phylum: Chordata
Class: Sauropsida
Subclass: Anapsida
Order: Testudines
Suborder: †Proganochelydia
Family: †**Odontochelyidae**
Li et al., 2008

Genus: †*Odontochelys*
Li et al., 2008

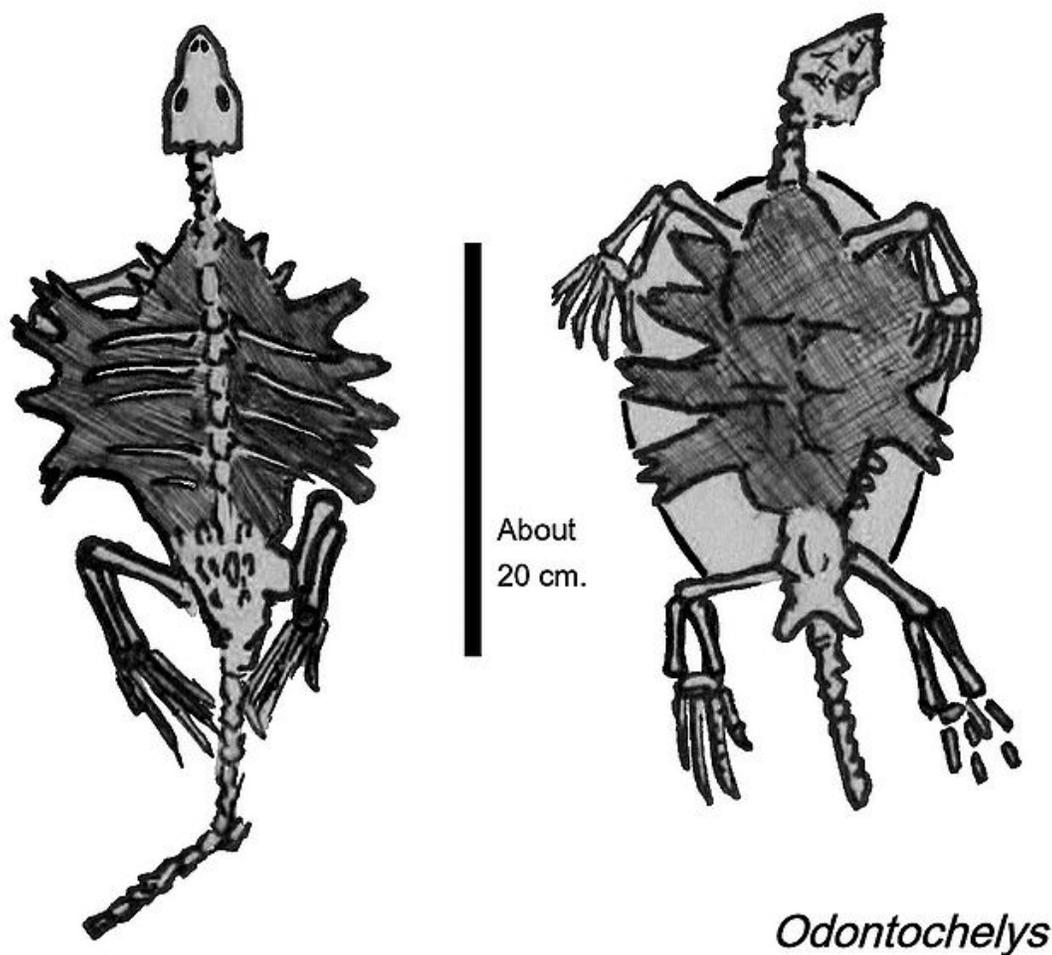
Species: †*O. semitestacea*

Binomial name

†*Odontochelys semitestacea*
Li et al., 2008

Odontochelys semitestacea is the oldest known turtle to have been discovered. It is the only known species in the genus *Odontochelys* and the family **Odontochelyidae**. The species was first described from three 220 million year-old specimens excavated in Triassic deposits originating from Guizhou, China.

As a primitive turtle, *Odontochelys* grossly differed from modern turtles in several ways. Modern turtles possess a horny beak without any teeth in their mouth. In contrast, *Odontochelys* fossils were found to have had teeth embedded in their upper and lower jaws. One of the most striking features of turtles, both modern and prehistoric alike, are their dorsal shells, forming an armored carapace over the body of the animal. *Odontochelys* only possessed the bottom portion of a turtle's armor, the plastron. It did not yet have a solid carapace as most other turtles do. Instead of a solid carapace, *Odontochelys* possessed broadened ribs like those of modern turtle embryos that still have not started developing the ossified plates of a carapace.



Sketch of *Odontochelys* fossil.

Aside from the presence of teeth and the absence of a solid carapace, a few other skeletal traits distinguish *Odontochelys* as basal compared to other turtles, extant and otherwise. The point of articulation between the dorsal ribs and the vertebrae are decidedly different in *Odontochelys* than in later turtles. In a comparison of skull proportions, the skull of *Odontochelys* is far more elongated pre-orbitally (in front of the eyes) compared to other turtles. The tail of the prehistoric turtle was longer in proportion to its body than other turtles. In addition, the transverse processes found in the tail are not fused such as in later turtles. Also, the scapulae of the examined specimens were identified to lack acromion processes. Taken together, these anatomical differences have been interpreted by the discoverers to mean that *Odontochelys* has some of the most primitive features ever seen in a turtle and is somewhat of a transitional fossil. Some scientists, however, are skeptical of this idea. Reisz and Head propose that *Odontochelys* does not represent a turtle with a partly evolved shell, but that it is a descendant of an older, land-living turtle, and that the shell became reversed. Such shells can be seen on modern turtles, like the leatherback turtles (the genus *Dermochelys*).

It is likely that *Odontochelys* was aquatic, as the fossil specimens were found in marine deposits rife with conodonts and ammonites. It is theorized that the primitive turtle frequented shallow marine waters close to shore.

The species' name, *Odontochelys semitestacea* literally means "toothed turtle with a half-shell" - an apt description of its most striking physical characteristics.

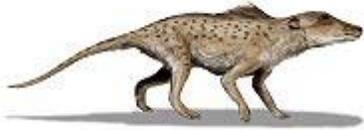
Chapter 8

Pakicetus and Psarolepis

Pakicetus

Pakicetus

Temporal range: Early Eocene



Pakicetus life restoration.

Scientific classification

Domain: Eukaryota

Kingdom: Animalia

Phylum: Chordata

Class: Mammalia

Order: Cetacea

Suborder: Archaeoceti

Family: Pakicetidae

Subfamily: Pakicetinae

Pakicetus

Genus: Gingerich & Russell,
1981

Species

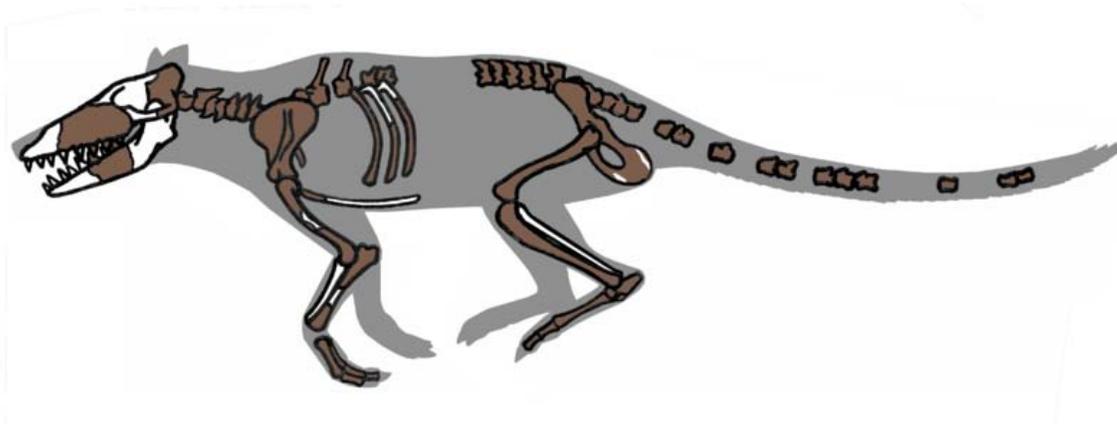
- *P. inachus* Gingerich & Russell, 1981 (type)
- *P. attockii* (West, 1980)
- *P. calcis* Cooper *et al.*, 2009
- *P. chittas* Cooper *et al.*,

Pakicetus is a genus of extinct terrestrial carnivorous mammal of the family Pakicetidae which was endemic to Pakistan from the Eocene (55.8 ± 0.2 — 40 ± 0.1 Ma). *Pakicetus* existed for approximately 15.8 million years. Many paleontologists regard it as a close relative to the direct ancestors of modern day whales.

Taxonomy



Pakicetus skull



Fossil remains of *Pakicetus* (after Thewissen et.al, 2001)

Pakicetus was assigned to Protocetidae by Gingerich and Russell (1981), Carroll (1988) and Benton (1993). Then to Pakicetinae by Gingerich and Russell (1990) and McKenna

and Bell (1997); and to Pakicetidae by Thewissen and Hussain (1998), Thewissen et al. (2001), Thewissen et al. (2001), Geisler and Sanders (2003), McLeod and Barnes (2008) and Uhen (2010).

Fossil distribution

The first fossils were uncovered in Pakistan, hence their name. The strata of western Pakistan where the fossils were found was then the coastal region of the Tethys Sea. The first fossil found of the creature consisted of an incomplete skull with a skull cap and a broken mandible with some teeth. It was thought to be from a mesonychid, but Gingerich and Russell recognized it as an early cetacean from characteristic features of the inner ear, found only in cetaceans: the large auditory bulla is formed from the ectotympanic bone only. This suggests that it is a transitional species between extinct land mammals and modern cetaceans. It was restored on the cover of *Science* as a semiaquatic, somewhat crocodilelike mammal, diving after fish.

Semi-aquatic or not?

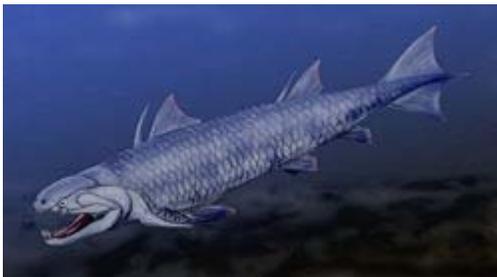
Somewhat more complete skeletal remains were discovered in 2001, prompting the view that *Pakicetus* was primarily a land animal about the size of a wolf, and very similar in form to the related mesonychids. In 2001, J. G. M. Thewissen and colleagues wrote that "Pakicetids were terrestrial mammals, no more amphibious than a tapir."

However, in 2009 Thewissen *et al* argued that "the orbits ... of these cetaceans were located close together on top of the skull, as is common in aquatic animals that live in water but look at emerged objects. Just like *Indohyus*, limb bones of pakicetids are osteosclerotic, also suggestive of aquatic habitat" (since heavy bones provide ballast).

Psarolepis

Psarolepis

Temporal range: Pridoli–Lochkovian



Psarolepis romeri

Scientific classification

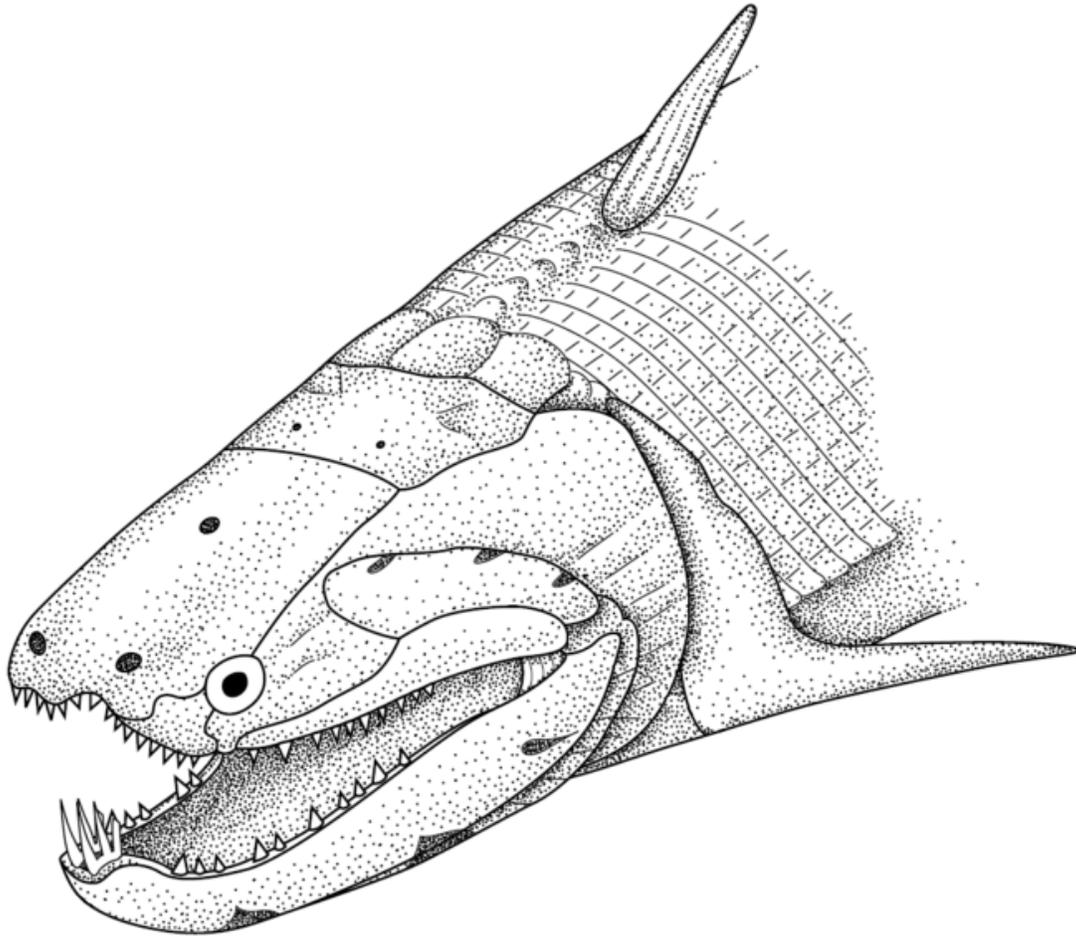
Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Class: Sarcopterygii
Order: ?Onychodontiformes
Family: *Incertae sedis*
Genus: ***Psarolepis***
Yu, 1998

Species

- *P. romeri* Yu, 1998 (type)

Psarolepis is a genus of extinct lobe-finned fish which lived around 397 to 418 million years ago (Pridoli to Lochkovian stages). Fossils of *Psarolepis* have been found mainly in South China and described by paleontologist Xiaobo Yu in 1998. It is not known certainly in which group *Psarolepis* belongs, but paleontologists agree that it probably is a basal genus and seems to be close to the common ancestor of lobe-finned and ray-finned fishes. In 2001, paleontologist John A. Long compared *Psarolepis* with Onychodontiform fishes and refer to their relationships.

Description



The head of *Psarolepis*.

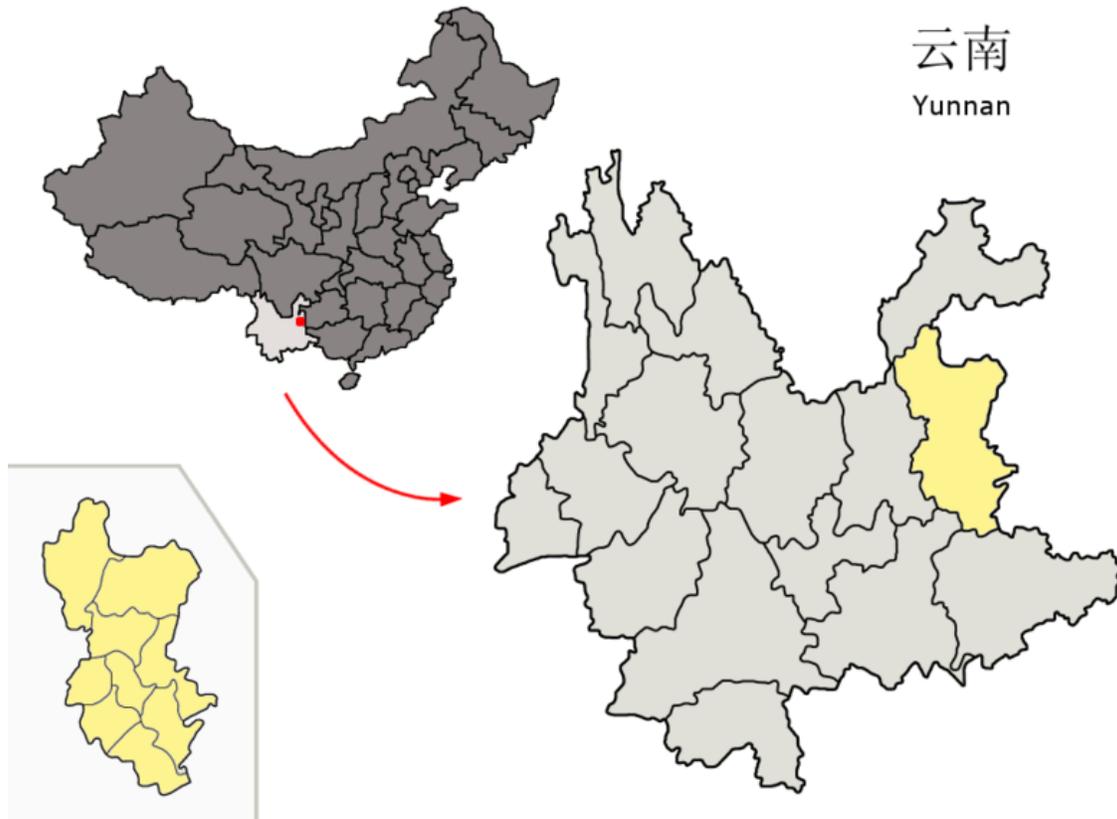
Psarolepis had a pair of 'parasymphysical tooth whorls', teeth which extend up at the front of the lower jaw. The head was made of several thick dermal plates and covered with deep pock-marks and large pores. Another trait is a large pectoral spine, just in front of the pectoral fin, extending back from the shoulder girdle, and a dorsal spine located in front of a median fin behind the head, which gives the fish a shark-like form.

The pock-marked head of *Psarolepis* was made of plates containing a layer of porcelain-like cosmine. Because the cosmine layer obscures the suture lines of the skull, it is difficult to study the exact bone structure. The snout was strangely humped and the nostrils were located above the eyes, which were just above the upper jaw.

The most spectacular findings were the fin spines. Two are known: one extending back from the shoulder girdle and another which is associated with the dorsal fin. These fin spines are found only in primitive jawed fishes and are apparently absent from the most primitive sharks, but present in abundance in more derived forms.

Psarolepis had teeth at the very front of the snout with large fangs on the tooth plate. Outstanding features are the 'parasymphysical tooth whorls' which place the fish in the order of onychodontida. The premaxilla and the dentary had large inner teeth and irregular array of tiny outer teeth.

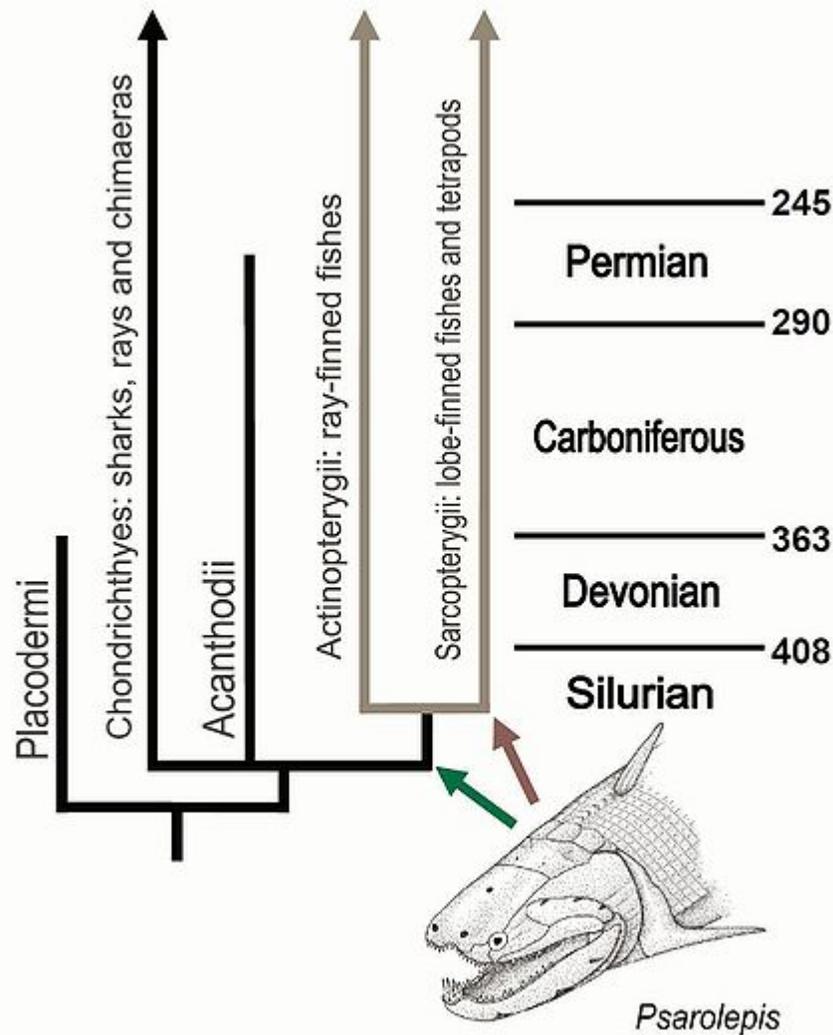
Discovery



Location of Qujing Prefecture (yellow) within Yunnan province of China, where the fossils of *Psarolepis* were discovered.

Most of the fossils of *Psarolepis* were discovered at the same locality of the Yulongsi, Xishancun and Xitun formations, about 10 km northwest of the city of Qujing, Yunnan, China. With this discovery other prehistoric lobe-finned fishes came to light such as *Youngolepis* and *Diabolepis*. The remains of *Psarolepis* were collected in 1981 and 1984 by paleontologist Min Zhu and colleagues and dated from Early Devonian and Late Silurian periods. Other fossils, also dated from Late Silurian, have been found in Vietnam but the description of the fish was based on the materials from China because they were better preserved.

History and classification



Fish relationships and the ambiguous position of *Psarolepis*. The red arrow shows *Psarolepis* as basal lobe-finned and the green arrow locates the fish as the basalmost bony fish.

When *Psarolepis* was described for the first time in 1998, it was placed in the group of sarcopterygians (lobe-finned fishes) because the skull and jaws resemble those of primitive lungfishes. In 1999 Zhu et al. were unable to locate *Psarolepis* in the cladogram because they did not know if it was the most primitive lobed-finned fish or the most primitive bony fish.

There are some characteristics that bony fish do not have, such as the median spine located behind the head, which is known in sharks and acanthodians, and the pectoral spine extending back from the shoulder girdle which is found in some placoderms and acanthodians. Later, in 2001, Zhu and Schultze gave more basis to the theory that *Psarolepis* was probably a basal bony fish.

The same year Long re-examined the phylogenetic position of the fish and pointed out several similarities between *Psarolepis* and Onychodontiform fishes. He also noted that the presence of a rotational tooth whorl combined with the other characteristics in the skull, and possibly in the shoulder girdle, show that *Psarolepis* is better placed as a sister taxon to *Onychodus* as the most basal member of the group of Onychodontiforms. Moreover, Long, referring to new fossils collected from Gogo Formation, Western Australia, said that *Psarolepis* and *Onychodus* are both basal bony fish and are more primitive than other lobe-finned groups.

Chapter 9

Puijila and Sivapithecus

Puijila

Puijila

Temporal range: Late Oligocene–Early Miocene



Puijila darwini

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Carnivora
Suborder:	Pinnipedia
Family:	
Genus:	<i>Puijila</i>

Species

- *P. darwini* (type)

Puijila darwini is an extinct species of pinniped which lived during the Miocene epoch about 21 to 24 million years ago. Approximately a metre (three feet) in length, the animal

possessed only minimal physical adaptations for swimming. Unlike modern pinnipeds, it did not have flippers and its overall form was otter-like, albeit more specialized; its skull and teeth are the features that most clearly indicate that it is a seal. It is considered to be the most primitive member of the seal family yet found. The genus name is an Inuktitut word for a young seal; the species name honours the English naturalist Charles Darwin. The one known specimen is a nearly complete fossilised skeleton. It is being housed at the Canadian Museum of Nature in Ottawa, Ontario.

Background



Skeleton

Puijila darwini was a semi-aquatic carnivore which represents a morphological link in early pinniped evolution. Its fossil remains demonstrate the presence of enlarged, probably webbed feet, robust forelimbs and an unspecialized tail. This suggests that *Puijila* swam quadrupedally using its webbed fore and hind feet for propulsion. Phylogenetic studies including molecular evidence suggest a sister relationship between pinnipeds (seals) and ursoids (bears) as well as musteloids (weasels and otters). It had been popularly assumed that land-dwelling mammals had at some point transitioned to a more marine existence, in essence "returning to the sea" in order to gain some sort of survival advantage. However, fossil evidence of this transition had been weak or contentious. The discovery of *Puijila* is important as it represents a morphological link in early pinniped evolution, and one that appears morphologically, to precede the more

familiarly structured *Enaliarctos* genus, despite apparently being a younger genus. In other words, *Puijila* is a transitional fossil that provides information about how the seal family returned to the seas, similar to the way that *Archaeopteryx* illuminates the origin of modern birds.

Discovery



Life restoration of *Puijila darwini*.

This novel species was discovered in 2007 by Natalia Rybczynski and her team using surface collection and screening at an early Miocene lake deposit of the Haughton Formation of Devon Island in Nunavut, Canada. The palaeobotanical record suggests that the palaeoenvironment around the lake comprised a forest community transitional between a boreal and a conifer–hardwood forest, in a cool temperate, coastal climate with moderate winters. *Puijila darwini* is the first mammalian carnivore found in the Haughton lake deposits. This also gives an indication that the entire pinniped family may have originated in the Arctic.

The initial find is credited to field assistant Elizabeth Ross, and was partly a matter of luck. Ross had been unexpectedly stranded with the team's ATV which had run out of fuel several kilometers away from base camp. The brain case was discovered a year later on the first day of the 2008 field expedition by Martin Lipman, the team's photographer.

Sivapithecus

Sivapithecus

Temporal range: 12.5–8.5 Ma
Miocene



Sivapithecus indicus skull, Muséum national d'histoire naturelle, Paris

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Primates
Family:	Hominidae
Subfamily:	Ponginae
Genus:	<i>Sivapithecus</i>

Species

Sivapithecus indicus
Sivapithecus sivalensis
Sivapithecus parvada

Sivapithecus is a genus of extinct primates. Fossil remains of animals now assigned to this genus, dated from 12.5 million to 8.5 million years old in the Miocene, have been found since the 19th century in the Siwalik Hills in what is now India, Nepal, and Pakistan. Any one of the species in this genus may have been the ancestor to the modern orangutans.

Description

Sivapithecus was about 1.5 metres (4.9 ft) in body length, similar in size to a modern orangutan. In most respects, it would have resembled a chimpanzee, but its face was closer to that of an orangutan. The shape of its wrists and general body proportions suggest that it may have spent a significant amount of its time on the ground, as well as in trees. It had large canine teeth, and heavy molars, suggesting a diet of relatively tough food, such as seeds and savannah grasses.

Species

Currently three species are generally recognized. *Sivapithecus indicus* fossils date from about 12.5 million to 10.5 million years ago. *S. sivalensis* lived from 9.5 million to 8.5 million years ago. It was found at the Pothowar plateau in Pakistan as well as in parts of India.

The animal was about the size of a chimpanzee but had the facial morphology of an orangutan; it ate soft fruit (detected in the toothwear pattern) and was probably mainly arboreal.

In 1988 a third, significantly larger species was described and named *S. parvada* (dated at about 10 million years ago).

In 1982, David Pilbeam published a description of a significant fossil find — a large part of the face and jaw of a *Sivapithecus*. The specimen bore many similarities to the orangutan skull and strengthened the theory (previously suggested by others) that *Sivapithecus* was closely related to orangutans.

Ramapithecus

Siwalik specimens once assigned to the genus *Ramapithecus* are now considered by most researchers to belong to one or more species of *Sivapithecus*. *Ramapithecus* is no longer regarded as a likely ancestor of humans.

The first incomplete specimens of *Ramapithecus* were found in Nepal on the bank of Tinau River western part of the country in 1932. The finder (G. Edward Lewis) claimed that the jaw was more like a human's than any other fossil ape then known. In the 1960s this claim was revived. At that time, it was believed that the ancestors of humans had diverged from other apes 14 million years ago. Biochemical studies upset this view,

suggesting that there was an early split between orangutan ancestors and the common ancestors of chimps, gorillas and humans.

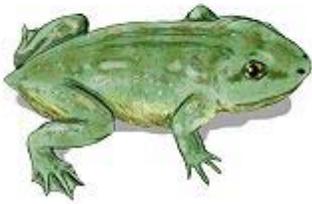
Meanwhile, more complete specimens of *Ramapithecus* were found in 1975 and 1976, which showed that it was less human-like than had been thought. It began to look more and more like *Sivapithecus* - meaning that the older name must take priority. It could be that *Ramapithecus* was just the female form of *Sivapithecus*. They were definitely members of the same genus. It is also likely that they were already separate from the common ancestor of chimps, gorillas and humans, which may be represented by the prehistoric great ape, *Nakalipithecus nakayamai*.

Chapter 10

Triadobatrachus and Westlothiana

Triadobatrachus

Triadobatrachus
Temporal range: Early Triassic



Artist's rendering of
Triadobatrachus sp.

Conservation status

Fossil

Scientific classification

Kingdom: Animalia
Phylum: Chordata
Class: Amphibia
Order: Anura
Family: Protobatrachidae
Genus: *Triadobatrachus*
Species: *T. massinoti*

Binomial name

Triadobatrachus massinoti

Triadobatrachus ('triple-frog') is an extinct genus of frog-like amphibian, including only one known species, *Triadobatrachus massinoti*. It is the oldest frog known to science, and an excellent example of a transitional fossil. It lived during the Early Triassic, in what is now Madagascar.



Artist's rendering of *Triadobatrachus massinoti*

Triadobatrachus was 10 centimetres (3.9 in) long, and still retained many primitive characteristics, such as possessing fourteen vertebrae, where modern frogs have only four to nine. Six of these vertebrae formed a short tail, which the animal retained as an adult. It probably swam by kicking its hind legs, although it could not jump, as most modern frogs can. Its skull resembled that of modern frogs, consisting of a latticework of thin bones separated by large openings. As evidenced by its large ear openings, *Triadobatrachus* possessed good hearing.

This creature, or a cousin, evolved eventually into modern frogs, the earliest example of which is *Sanyanlichan*, millions of years later in the late Jurassic.

It was first discovered on 1937, when Adrien Massinot, near the village of Betsieka in northern Madagascar, found an almost complete skeleton. The animal must have fossilized soon after its death, because all bones lay in their natural position. Only the anterior part of the skull and the ends of the limbs were missing.

Although it was found in marine deposits, the general structure of *Triadobatrachus* shows that it may have lived for part of the time on land and breathed air. Its proximity to the mainland is further borne out by the remains of terrestrial plants found together with it.

Westlothiana

Westlothiana

Temporal range: Early Carboniferous



Westlothiana lizziae

Scientific classification

Kingdom: Animalia
Phylum: Chordata
Class: Amphibia/Reptilia
Order: Cotylosauria?
Genus: *Westlothiana*
Species: *W. lizziae*

Binomial name

Westlothiana lizziae
Smithson and Rolfe, 1990

Westlothiana lizziae was a reptile-like amphibian or possibly early reptile that bore a superficial resemblance to modern-day lizards. It lived during the Carboniferous period, about 350 million years ago. The type specimen was discovered in East Kirkton Quarry, Bathgate, Scotland, in 1984, and was named after the West Lothian district where it was found. *Westlothiana's* anatomy contained a mixture of both labyrinthodont and reptilian features, and was originally regarded as the first reptile. Most scientists place them among the Reptilomorpha, as a sister group to the first amniotes.

Westlothiana *in life*

This species probably lived near a freshwater lake, probably hunting for other small creatures that lived in the same habitat. It was a slender animal, with rather small legs and a long tail. Together with *Casineria*, another transitional fossil found in Scotland, it is

one of the smallest reptil-like amphibians known, being a mere 20 cm in adult length. The small size has made it a key fossil in the search for the earliest amniote, as amniote eggs are thought to have evolved in very small animals. Advanced features that ties it in with the reptilian rather than amphibian group is unfused ankle bones, lack of labyrinthodont infolding of the dentin, a lack of an otic notch and a generally small skull.

Ruta & al. (2003) interpreted the long body and small legs as a possible adaption to burrowing, similar to that seen in modern skinks.

Phylogeny

The phylogenetic placement of *Westlothiana* has varied from basal amniote (i.e. a primitive reptile) to an amphibian Lepospondyl only distantly related to the Reptiliomorpha. The actual phyllogenetic position of *Westlothiana* is uncertain, reflecting the uncertainty of labyrinthodont phylogeny in general.

Chapter 11

Lucy (Australopithecus)

Lucy



Catalog number AL 288-1

Common name Lucy

Species	<i>Australopithecus afarensis</i>
Age	3.2 million years
Place discovered	Afar Depression, Ethiopia
Date discovered	November 24, 1974
Discovered by	Donald Johanson Maurice Taieb Yves Coppens Tom Gray

Lucy (also given a second (Amharic) name: *dinqineš*, or *Dinkenesh*, meaning "you are amazing") is the common name of **AL 288-1**, several hundred pieces of bone representing about 40% of the skeleton of an individual *Australopithecus afarensis*. The specimen was discovered in 1974 at Hadar in the Awash Valley of Ethiopia's Afar Depression. Lucy is estimated to have lived 3.2 million years ago. The discovery of this hominid was significant as the skeleton shows evidence of small skull capacity akin to that of apes and of bipedal upright walk akin to that of humans, providing further evidence supporting the view that bipedalism preceded increase in brain size in human evolution, though other findings have been interpreted as suggesting that *Australopithecus afarensis* was not directly ancestral to humans. In 1994, a new hominid, Ardi, was found, pushing back the earliest known hominid date to 4.4 million years ago, although details of this discovery were not published until October 2009.

Discovery



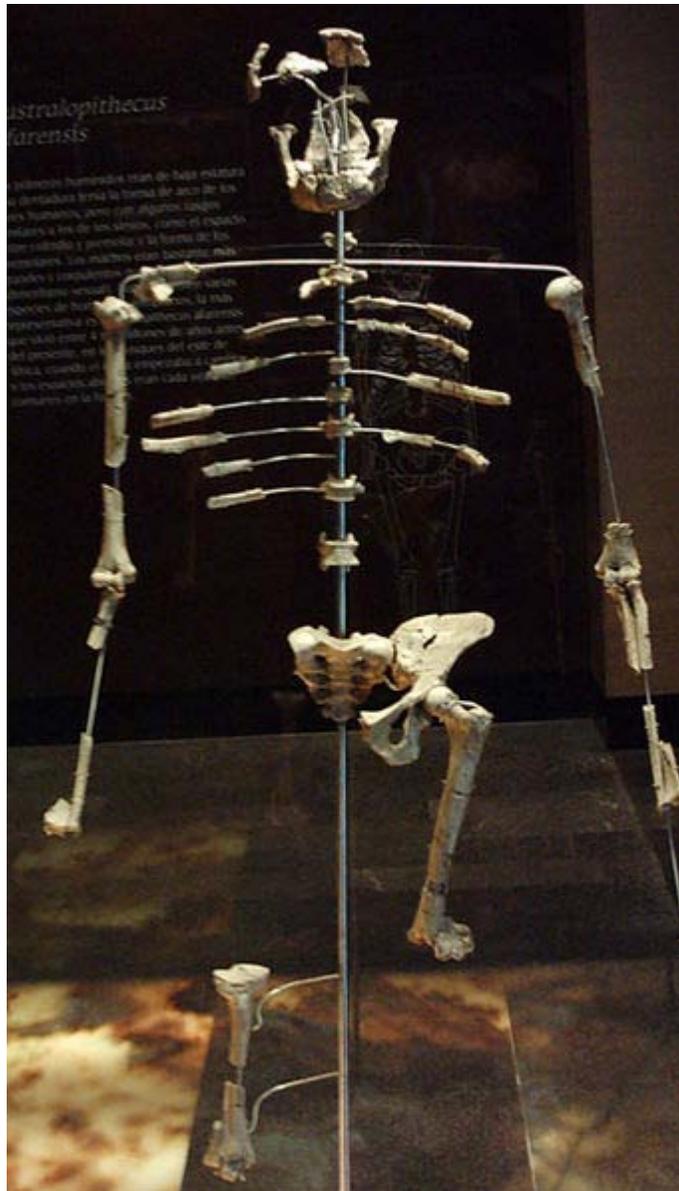
Side view of Lucy replica

French geologist Maurice Taieb discovered the Hadar Formation in the Afar Triangle of Ethiopia in 1972. He then formed the International Afar Research Expedition (IARE), inviting three scientists from three countries to co-direct the research. These were Donald Johanson, an American anthropologist, and Founding Director of the Institute of Human Origins of Arizona State University; the famous British archaeologist Mary Leakey; and Yves Coppens, a French born paleontologist now based at the Collège de France. An expedition was formed with four American and seven French participants, and in the autumn of 1973 the team surveyed Hadar for fossils and artifacts related to the origin of humans.

In November 1973, near the end of the first field season, Johanson noticed a fossil of the upper end of a shinbone, which had been sliced slightly at the front. The lower end of a femur was found near it, and when he fitted them together the angle of the knee joint clearly showed that this fossil, reference AL 129-1, was an upright walking hominid. The fossil was over three million years old, much older than any others known at the time. The site lay about 2.5 kilometres (1.6 mi) from the site where they subsequently found "Lucy".

The team returned for the second field season in the following year and found hominid jaws. Then, on the morning of November 24, 1974, near the Awash River, Johanson abandoned a plan to update his field notes and joined graduate student Tom Gray to search Locality 162 for bone fossils.

Both Donald Johanson and Tom Gray spent two hours on the increasingly hot arid plain, surveying the dusty terrain, then Johanson decided on a hunch to make a small detour on their way back to their vehicle to look at the bottom of a small gully that had been checked at least twice before by other workers. At first sight there was nothing immediately visible, but as they turned to leave, a fossil caught Johanson's eye: an arm bone fragment lying on the slope. Near it lay a fragment from the back of a small skull. They noticed part of a femur (thigh bone) a few feet (around 1 m) away. As they looked further, they found more and more bones on the slope, including vertebrae, part of a pelvis, ribs, and pieces of jaw. They marked the spot and returned to camp, excited at finding so many pieces apparently from one individual hominid.



Cast of Lucy in Mexico

In the afternoon, everyone on the expedition was at the gully, sectioning off the site and preparing for careful collection which eventually took three weeks. That first evening they celebrated at the camp, staying up all night, and at some stage during the evening the fossil AL 288-1 was nicknamed **Lucy**, after the Beatles song "Lucy in the Sky with Diamonds", which was being played loudly and repeatedly on a tape recorder in the camp.

Over the next three weeks, several hundred pieces or fragments of bone were found, with no duplication, confirming their original speculation that they were from a single skeleton. As the team analyzed the fossil further, they calculated that an amazing 40% of a hominid skeleton had been recovered, an astounding feat of anthropology. Usually,

only fossil fragments are discovered; rarely are skulls or ribs found intact. Johanson considered it was female, based on the one complete pelvic bone and sacrum indicating the width of the pelvic opening. Lucy was only 1.1 m (3 ft 7 ½ in) tall, weighed 29 kg (64 lb) and looked somewhat like a Common Chimpanzee, but although the creature had a small brain, the pelvis and leg bones were almost identical in function to those of modern humans, showing with certainty that these hominids had walked erect. Under an agreement with the government of Ethiopia, Johanson brought the skeleton back to Cleveland where it was reconstructed by Owen Lovejoy. It was returned to Ethiopia according to agreement some 9 years later. Lucy as a fossil hominid captured public notice, becoming almost a household name at the time.

Further discoveries of *A. afarensis* specimens occurred during the 1970s, giving anthropologists a much better appreciation of the range of variability and sexual dimorphism of the species.

Notable characteristics

Postcranial



Lucy skeleton reconstruction. Cleveland Museum of Natural History

One of Lucy's most striking characteristics is a valgus knee, which indicates that she normally moved by walking upright. Her femoral head was small and her femoral neck was short, both primitive characteristics. Her greater trochanter, however, was clearly derived, being short and human-like rather than taller than the femoral head. The length ratio of her humerus to femur was 84.6% compared to 71.8% for modern humans and 97.8% for Common Chimpanzees, indicating that either the arms of *A. afarensis* were beginning to shorten, the legs were beginning to lengthen, or both were occurring

simultaneously. Lucy also had a lumbar curve, another indicator of habitual bipedalism. Lucy likely had non-pathological (physiologic) flat feet, not to be confused with pes planus, though other *afarensis* individuals appear to have had arched feet.

Pelvic girdle

Johanson recovered Lucy's left innominate bone and sacrum. Though the sacrum was remarkably well preserved, the innominate was distorted, leading to two different reconstructions. The first reconstruction had little iliac flare and virtually no anterior wrap, creating an ilium that greatly resembled that of an ape. However, this reconstruction proved to be faulty, as the superior pubic rami would not have been able to connect if the right ilium was identical to the left. A later reconstruction by Tim White showed a broad iliac flare and a definite anterior wrap, indicating that Lucy had an unusually broad inner acetabular distance and unusually long superior pubic rami. Her pubic arch was over 90 degrees, similar to modern human females. Her acetabulum, however, was small and primitive.

Cranial specimens

The cranial evidence recovered from Lucy is far less derived than her postcranium. Her neurocranium is small and primitive, while she possesses more spatulate canines than apes. The cranial capacity was about 375 to 500 cc.

Other findings

A study of the mandibular structure of a number of specimens of *Au. Afarensis* indicated that Lucy's jaw was rather unlike other hominins, having a more gorilla-like appearance. Rak *et al.* consider that this mandible structure arose "independently in gorillas and hominins", but that *Au. Afarensis* is therefore "too derived to occupy a position as a common ancestor of both the *Homo* and robust australopith clades".

Exhibitions

Lucy is preserved at the National Museum of Ethiopia in Addis Ababa. A plaster replica is displayed instead of the original skeleton. A cast of the original skeleton in its reconstructed form remains on display at the Cleveland Museum of Natural History. A diorama of *Australopithecus afarensis* and other human predecessors showing each species in its habitat and demonstrating the behaviors and capabilities that scientists believe it had is displayed in the Hall of Human Biology and Evolution at the American Museum of Natural History in New York City. A cast of Lucy's skeleton as well as a reconstruction of Lucy is on display at The Field Museum in Chicago in their Evolving Planet exhibition.

US tour

A six-year exhibition tour of the United States, titled *Lucy's Legacy: The Hidden Treasures of Ethiopia*, features the *Lucy* fossil as well as over 100 artifacts from ancient times to the present, is currently underway. The tour was approved by the Ethiopian government and organized in collaboration with the Houston Museum of Natural Science, where it had been on display from August 31, 2007 until September 1, 2008. An undisclosed proportion of the proceeds from the tour is to go toward modernizing Ethiopia's museums. The U.S. Department of State also approved the tour. There was controversy in advance of the tour over concerns about the fragility of the specimens, with various experts including paleoanthropologist Owen Lovejoy and anthropologist and conservationist Richard Leakey publicly stating their opposition. The Smithsonian Institution and Cleveland Museum of Natural History were among museums declining to host the exhibits. The fossil's discoverer Don Johanson stated that although he was somewhat uneasy about the possibility of damage, he did not oppose exhibiting *Lucy* as it will help to raise awareness of human-origins studies. The museum is making arrangements for the exhibits to be shown at as many as ten other museums. The exhibit was shown at the Pacific Science Center in Seattle, Washington where it was displayed from October 4, 2008 - March 8, 2009. In September 2008, between the exhibits in Houston and Seattle, the fossils were taken to the University of Texas at Austin for 10 days to complete the first ever high resolution CT scan of the fossil.

Lucy has been open at Discovery Times Square Exposition, a new facility located in New York City since June 24, 2009. The *Australopithecus afarensis* was on display until October 25, 2009. In New York, the exhibition will include *Ida* (Plate B), the other half of the recently announced *Darwinius masilae* fossil.