The First Birds:

An introduction to the prehistoric long-tailed birds

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Contents

Introduction: The Urvogel

The Berlin Archaeopteryx *specimen. Image from Wikipedia, photograph by Raimond Spekking.* ***GNU Free Documentation license****, Version 1.2*

Prehistoric birds are often overshadowed in the public consciousness by their larger dinosaurian relatives; *Triceratops*, *T. rex*, and a decidedly un-birdlike (fictional) portrayal of "raptors" dominate the prehistoric landscape in popular culture from film to TV to video games. Ask even enthusiastic young dinosaur fans to name a few prehistoric birds, and most will be stumped after the obvious choice: *Archaeopteryx*, the famous "first bird" (or "urvogel", an increasingly popular term for the Bavarian fossil). However, we now know that Mesozoic birds were incredibly diverse, and discoveries since the late 1990s have shown to be included among them some of the most popular and well-known dinosaurs.

The first *Archaeopteryx* fossil, and in fact the first Mesozoic bird fossil ever found under just about any definition of the term (see below), was described by Hermann von Meyer in 1861. Consisting of a single fossil feather unearthed in the Solnhofen limestone quarries of Bavaria, this historic find is now housed in the collections of the Humboldt Museum in Berlin. Complete skeletons soon followed, and revealed something much different than modern birds.[1] *Archaeopteryx lithographica* ("lithographic ancient bird", referring to the use of the limestones it was preserved in for lithographic printing) had a long tail, like a reptile, no apparent beak, numerous small teeth, and clawed fingers, among other primitive features. Subsequent discoveries of small dinosaurs would show striking similarities to *Archaeopteryx*, leading to the hypothesis that dinosaurs and birds were close relatives.[2] This hypothesis would be strengthened with the discovery of species like *Deinonychus*, which were so similar to *Archaeopteryx* some scientists placed them in the same biological family.[3] Today, a vast

majority of scientists hold the opinion that birds are so similar to dinosaurs they are the dinosaur's direct descendants--birds are as much dinosaurs as the long-necked elephantine sauropods are.[4]

What is a Bird?

Pretenders to *Archaeopteryx*'s title of "first bird" have come and gone over the past several decades (most infamous of these is the still-contentious *Protoavis*, which is likely to be a chimera made up of remains from various reptiles including dinosaurs and prolacertiforms).[5] Despite the dubious nature of this challenger, *Archaeopteryx* has retained its title largely because of the nature of classification itself. Historically, the term "bird" has become strongly associated with the group Aves, named by Carolus Linnaeus (widely regarded as the father of biological classification) in 1758. Linnaeus designated Class Aves (which means "birds" in Latin) as one of the major divisions of life, ranked highly in his famous system of taxonomy (the familiar hierarchy of Kingdom, Phylum, Class, Order, Family, Genus, and Species), equal in status to mammals (Class Mammalia) and Reptiles (class Reptilia) among the animals with backbones (Phylum Chordata).[6]

After centuries of use, Linnaeus' system of classification began to show its age. By in the 1960s, biologists had become increasingly dissatisfied with various incompatibilities between the Linnaean system and evolutionary theory (Linnaeus had, after all, devised it before Darwin demonstrated the common descent of life). Over the next several decades, many scientists, especially those working in the field of vertebrate paleontology, would largely abandon the Linnaean system in favor of one based on ***clades*** (groups containing certain species, their common evolutionary ancestor, and all other descendants of that ancestor, no matter how modified from the original form).[7]

Defining Aves

The use of clades in place of ranked classes addressed another shortcoming of the Linnaean system: lack of definitions. Linnaean classes were determined by a vague set of characteristics and had no set definitions, making their use often subjective and not scientific. Clades, on the other hand, are required to have definitions, and are defined not by characteristics, but by content.[7] In phylogenetic naming, Mammalia doesn't mean 'a warm-

blooded vertebrate with hair that feeds its young with milk,' but rather 'the group of vertebrates that contains placentals, monotremes, and marsupials, their common ancestor, and all other descendents of that ancestor, either known now or to be discovered later.'

(This shift from using vague, know-it-when-you-see-it characteristics to hard and fast, quantifiable definitions, is similar to the controversial re-definition of 'Planet' that occurred in 2006.)

Applying this to birds has proven divisive. Originally, scientists like Jaques Gauthier (one of the fathers of cladistic methods) defined Aves the way Mammalia came to be defined--as a "crown group", that is, the group containing all modern bird groups and any species closer to them than to more distantly related prehistoric lineages. This use of Aves preserves Linnaeus' usage (he didn't know of any prehistoric birds), but also excludes prehistoric birds such as *Archaeopteryx* and even species very similar to modern birds like *Ichthyornis*.[8] Subsequently, attempts were made to re-define Aves to include *Archaeopteryx* for historical reasons (after all, it has always been considered the "first bird").[9] Critics called these attempts arbitrary: why include *Archaeopteryx* and not it's closest relatives (such as *Microraptor*), which were more like modern birds in some respects?[8] As of this writing, a body known as the PhyloCode is being organized to govern the naming of clades, and it seems likely they will adopt the crown group usage as official.

Parts of a feather.
***1**. Vane. **2**. Rachis **3**. Barb*
***4**. Afterfeather **5**. Hollow shaft, calamus.*
Public domain from Wikipedia.

When this usage is officially adopted, it will leave most Mesozoic birds outside of Aves. This will only require a semantic change; "bird" will no longer be synonymous with Aves. Just as *T. rex* is a "non-avian dinosaur", *Ichthyornis* will be a "non-avian bird" (and, ironically, also a non-avian dinosaur, as all birds are included in the clade Dinosauria as a sub-

group).

So what is a bird? As a vernacular rather than scientific term, this is a matter of taste. Most definitions hinge on certain key aspects: egg-laying, feathers, and flight. If this usage is adopted, *Archaeopteryx* may still be a bird, depending on its controversial flight abilities. *Microraptor* is probably a bird as well. Of course, not all birds fly, and just as there are ground birds and flightless birds today, many Mesozoic lineages lost flight, or evolved before flight.

The First Birds

The earliest known bird, frond-tailed Anchiornis huxleyi*, was a member of the deinonychosaurian clade Troodontidae. Illustration by Matt Martyniuk Licensed under Creative Commons Attribution 3.0*

For over a century, *Archaeopteryx* had been considered the first (i.e. earliest known) bird, classified as such based the presence of feathered wings (whether or not they were used to fly). For decades, it remained not only the earliest, but the only Mesozoic animal known to possess the impression of feathers. By the time more were discovered in the 1990s, cladistics had all but replaced Linnaean classification in paleontology. Therefore, when more animals with feathers and wings were found in the late 1990s, they were not

considered birds, but rather feathered, non-avian dinosaurs (among paleontologists, the broad use of Aves was favored, and so no distinction was usually drawn between Aves and "birds"). Dinosaurs like *Sinornithosaurus* and *Microraptor*, despite having feathered wings and possibly flight, were not birds because they fell just outside the clade containing modern birds and *Archaeopteryx*. Either way, these fossils hailed from the Yixian and Juifotang formations of Early Cretaceous China, and were later than the Late Jurassic *Archaeopteryx*. Birds or not, Archie was still "first."

The discovery of feathered dinosaurs in the Chinese Dauhugou Beds muddied the waters. To date, three birds are known from the Daohugou Beds: *Pedopenna dauhugouensis*, *Scansoriopteryx heilmanni*, and *Epidexipteryx hui*.[10][11][12] The Dauhugou Beds date to earlier than the Yixian, but how much earlier is controversial. The average found in published scientific literature gives a Late Jurassic age, equal to or earlier than *Archaeopteryx*. Some studies suggest they are Middle Jurassic, which would make them solidly earlier than *Archaeopteryx*.[13] Again, the fossil animals here are slightly less advanced than Archie, and so wouldn't be considered birds under the broader definition of Aves. But with Aves and bird decoupled from each other, the Dauhugou birds enter contention.

The Daohugou bed birds ceded their titles as fist birds in 2009, when bird fossils were described from the even earlier Chinese Tiaojishan Formation, dating to between 161 and 155 million years ago, solidly earlier than *Archaeopteryx*. The first of these to be announced to the public was *Anchiornis*, a primitive troodontid. Like the Daohugou *Pedopenna* and the later *Microraptor*, *Anchiornis* possessed not only well-developed wings, but wing-like feather structures on the hind legs, strongly suggesting that all deinonychosaurs (and possibly, all modern bird) ultimately descended from gliding, four-winged forms.[14]

Frond-Tails, Ribbon-Tails and Fan-Tails

Despite their absence from popular media in favor of larger, scalier dinosaurs, Mesozoic birds were very diverse. As evidenced by early classification schemes, the first birds can generally be divided into two types: long-tailed and short tailed. Pre-cladistic classifications divided these into the subclasses Sauriurae ("lizard tails," for their long, bony, reptile-like tails) and Ornithurae ("bird tails," which had evolved the modern configuration of an extremely shortened tail).[8]

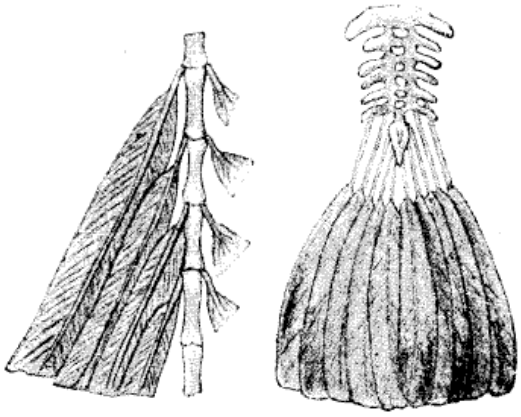


Illustration comparing the "frond-tail" of Archaeopteryx *to the "fan-tail" of a modern bird. This image was first published in the 2nd edition of the Swedish encyclopedia Nordisk familjebok (1904–1926), public domain.*

In his excellent 2006 book *Glorified Dinosaurs: The Origins and Early Evolution of Birds*, Luis Chiappe termed these two basic types "fan-tailed birds" and "frond-tailed birds," due to the distinct configuration of feathers differing tail length produced. On frond-tailed birds (the most primitive type), tail feathers (or ***retrices***) are generally arranged all along the length of the long skeletal tail, producing a shape similar to the frond of a fern. Modern birds are fan-tailed; due to the shortening of the tail, all tail feathers are anchored to a single bone, the ***pygostyle***, and so form a fan that the bird can often fold and unfold.[15]

Confuciusornis sanctus an early "ribbon-tailed" bird, by Matt Martyniuk, all rights reserved.

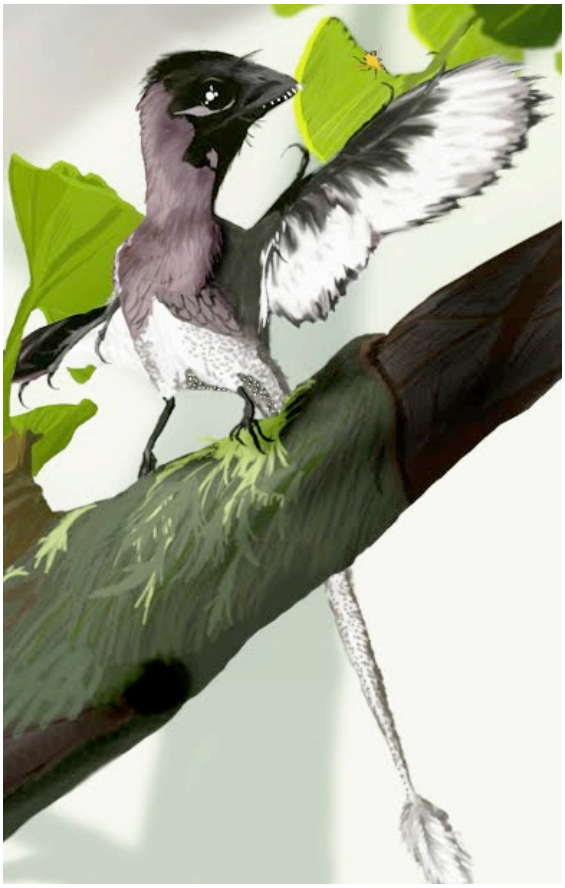
However, this distinction is not so cut and dry among Mesozoic birds. Some early birds, like *Microraptor* and *Jeholornis*, had sprays of feathers only at the tip of the long tail, blurring the distinction between frond tails and fan tails.[16] Also, the advent of the fan

tail itself seems to have come later than expected. Most early short-tailed birds, like *Confuciousornis* and the enantiornithines, only had one or two pairs of specialized streamer-like feathers on the tail. Otherwise, these birds lacked any long tail feathers, and their tails are merely fluffy stumps covered in down-like body feathers.[17] A new term, “Ribbon-Tailed Birds”, is needed for these intermediate forms. True fan-tailed birds seem to be more advanced, having arisen in the clade Ornithuromorpha.

The Long-Tailed Birds

Long-Tailed Bird Diversity

Details of the early diversification of long-tailed birds are obscure due to gaps in the fossil record. Modern feathers, consisting of a central shaft or ***rachis***, and surrounded by a ***vane*** of closely packed ***barbs***, are called known as ***pennaceous*** feathers. These first appeared in the common ancestor of the clade Aviremigia, a group containing the oviraptorosaurs, deinonychosaurs (the "raptors" of popular culture), and all more advanced types of bird (**avialans**).[18] The most primitive deinonychosaurs and most primitive oviraptorosaurs, both sides of the initial genetic split among birds, are very different, so estimating what their common ancestor might be like (the true "first bird") is difficult.



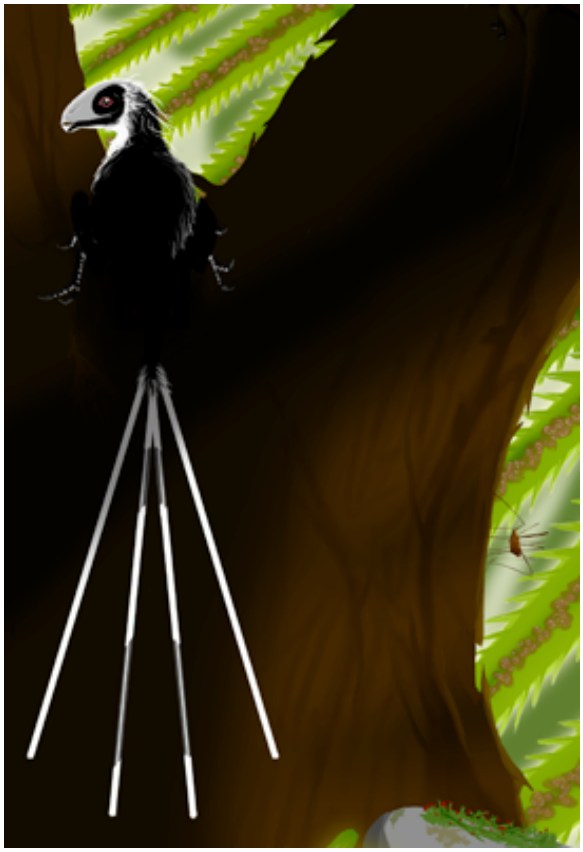
Digital painting of the Jurassic Scansoriopteryx heilmanni*, by Matt Martyniuk. Licensed under Creative Commons Attribution 3.0*

Scansors

Some of the earliest and most primitive members of the bird linage are the unusual scansoriopterygids, or "climbing wings." The first to be identified, *Scansoriopteryx* is known only from two juvenile specimens measuring a few inches long. These tiny

creatures had an unusual suite of primitive and avian features that initially led some scientists to conclude that not only were these the ancestors of all birds, but were more primitive than most other dinosaurs (mainly due to a hip lacking the characteristic perforated socket of all dinosaurs, which may be explained by the juvenile nature of the specimens).[26] *Scansoriopteryx* also had an unusual hand; unlike almost all other dinosaurs and birds, the third finger was longer than the second. It may have used this for probing for insects, like a modern aye-aye lemur, or for climbing, or both. Other features may have been related to a climbing lifestyle, like a large, low hallux toe (seen in modern perching birds but not more primitive forms).[11]

A second type of scansor, the first known adult specimen, was described in 2008. *Epidexipteryx* was notable for its unusual, large, forward-pointing teeth, lending additional support to the idea that these small birds fed on tree-dwelling insects. *Epidexipteryx* had a very short, bony tail with a fused, pygostyle-like tip, which it probably aquired independently of the later ribbon-tailed birds. Epidex's short, pseudo ribbon tail was used as support for a dramatic set of four highly elongated tail feathers (ETFs). Unlike tail feathers in true fan-tailed birds, the central quill of these ETFs supported a vane made up of a single ribbon-like sheet, rather than separate filaments linked by barbules. In this way they're structurally similar to the long display feathers of *Confuciousornis* and other ribbon-tailed birds.

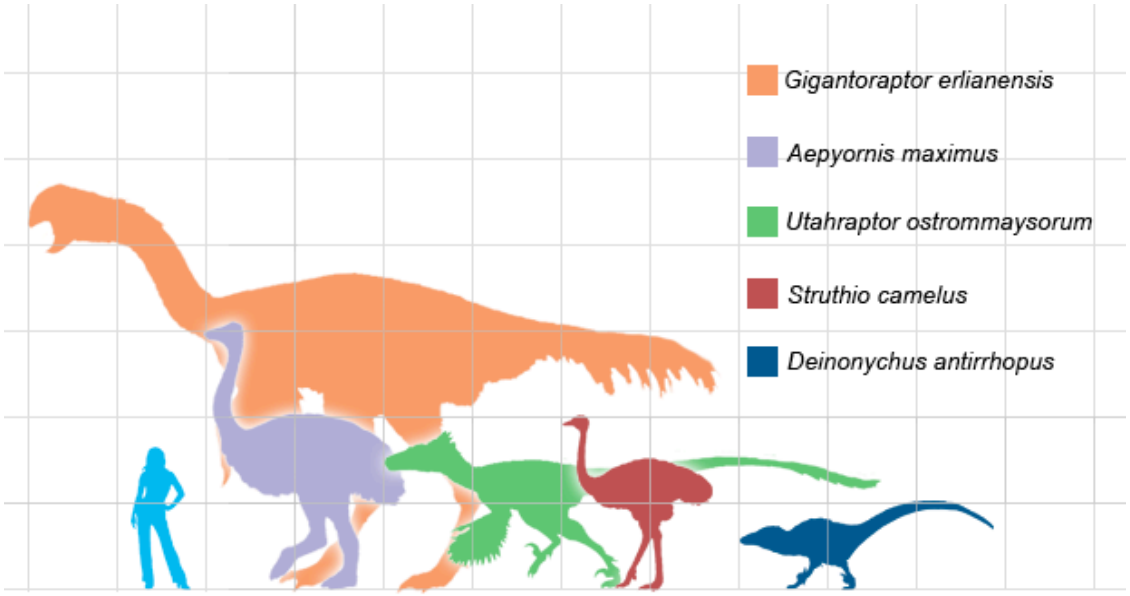


Digital painting of the pseudo-ribbon tailed bird Epidexipteryx hui*, by Matt Martyniuk, all rights reserved.*

All these unique features paint a picture of scansors as a bizarre offshoot of the original bird lineage, not direct ancestors of modern birds, and hint at the hidden diversity of birds waiting to be discovered in the Middle or Early Jurassic.

Oviraptorosaurs

A second strange offshoot of the early Mesozoic bird lineage are bizarre, omnivorous ground birds called the oviraptorosaurs. The most primitive forms, like *Caudipteryx*, were long legged, fairly short-armed, small herbivorous ground birds with mostly toothless beaks. More advanced oviraptorosaurs became larger, and some had elaborate casques on their beaks similar to modern Hornbills or Cassowaries. At least one grew to enormous sizes: *Gigantoraptor erlianensis*, at 1.4 tons,[19] is among the largest birds of all time.



Size comparison of select modern and Mesozoic giant ground birds by Matt Martyniuk. Each segmnt = 1 square metre. Licensed under Creative Commons Attribution 2.5

Most researchers, based on cladistic analysis, find the oviraptorosaurs to be more distantly related to modern birds than is *Archaeopteryx*. Despite this, they share some strikingly bird-like features that must otherwise be explained by convergent evolution: toothless beaks, shortened tails with pygostyles bearing fans of feathers, etc. Famously, several oviraptorids have been found brooding their nests as modern birds do. Especially due to the discovery of *Incisivosaurus*, many researchers had speculated that oviraptorosaurs were close relatives of the therizinosaurs, bizarre bird-like herbivorous dinosaurs with distinctively huge, scythe-shaped claws on their hands.

Contrary to what would be expected, impressions of feathers from therizinosaurs showed only basic filaments, unlike the advanced feathers of other maniraptors. This, as well as more detailed phylogenetic analysis, has shown therizinosaurs to be more primitive than true, wing-bearing birds.

Some scientists have gone the other way, disagreeing with the assessment of oviraptors as a primitive offshoot of birds, and believe them to actually be avialans closer to modern birds than *Archaeopteryx*. If this is the case, their beaks and short tails might be truly modern characteristics, rather than a separate development. This would also explain why the primitive oviraptorosaurs seem unlike their supposed close relatives, the deinonychosaurs (currently explained by lack of relevant "missing link" fossils).[20]

Profile of the oviraptorosaur Heyuannia huangi *by Matt Martyniuk. Licensed under* *Creative Commons Attribution 2.5*

Deinonychosaurs

Cast specimen of Microraptor zhaoianus*, photo by Matt Martyniuk. Licensed under* Creative Commons Attribution 2.5

The fossil record of early deinonychosaurs is relatively good, and primitive members of both major lineages (Troodontidae and Dromaeosauridae) are known from good fossil remains and feather impressions. Unsurprisingly, primitive members of each family are very similar to each other, and to *Archaeopteryx*, making it clear that both deinoncyhosaur lineages and the lineage leading to modern birds evolved from a common ancestor very much like *Sinovenator* (the most primitive known troodont), *Tianyuraptor* (the most primitive dromaeosaurid), or Archie itself (the most primitive known ***avialan***, birds more advanced than deinonychosaurs).[21] In fact, *Anchiornis*, the earliest known bird, was itself a primitive troodont deinonychosaur. However, given its genetic position as more advanced than oviraptorosaurs, it is likely that even earlier birds wait to be discovered.

Primitive deinonychosaurs appear to have been capable of gliding flight, with some taking steps toward powered, flapping flight. *Microraptor* and Anchiornis both have well-developed wings with an additional set of "hind wings" formed from vaned feathers on the lower legs and feet, which would have formed a biplane-like configuration when gliding or parachuting from trees. Both *Microraptor* and another deinonychosaur, *Rahonavis,* had wings large enough and powerful enough to have allowed clumsy, level bursts of flight, though at least in the case of *Microraptor*, gliding was probably the preferred mode of transport.[22] Deinonychosaurs also continued the trend of flightless ground birds becoming larger.[21] These later, larger deinonychosaurs include the famous "raptors," which did not actually resemble the reptilian monsters depicted in the movies, but were very large predatory birds, complete with substantial wings (evidence for this comes

from feather anchor ponts found on the "arm" bones of *Velociraptor* itself).[23] The "raptors" did not really resemble their carnosaurian cousins, but rather the later "terror birds", or an over sized predatory *Archaeopteryx*. As maniraptor expert Mark Norell, curator at the American Museum of Natural History stated in an interview on the subject:

Illustration of the deinonychosaur Microraptor zhaoianus *by Matt Martyniuk. Licensed under Creative Commons Attribution 2.5*

> *"The more that we learn about these animals the more we find that there is basically no difference between birds and their closely related dinosaur ancestors like velociraptor. Both have wishbones, brooded their nests, possess hollow bones, and were covered in feathers. If animals like velociraptor were alive today our first impression would be that they were just very unusual looking birds."*[24]

Even the characteristic enlarged "sickle claw" on the second toe of most deinonychosaurs probably did not begin as a weapon to hold and kill prey. Rather, their shape (and the shape of the forelimb claws) more closely matches the claws of climbing animals. The sickle claws and wing claws alike were also attached in a way ideal for transferring stress loads to the rest of the foot or wing, unlike the expected anatomy of a slicing weapon. It is likely that these claws were first used for climbing trees (like the crampons used by utility pole linemen) in small, gliding deinonychosaurs, and were later adapted for prey capture in their larger, ground-dwelling descendants.[25]

Avialans

Archaeopteryx and its relatives arose from the same stock as the deinonychosaurs, and from these, the line leading to modern birds arose. All birds closer to Aves than to deinonychosaurs are termed avialans ("bird wings"), though that name was based originally on a physical character (the presence of wings used for flight) and so might be replaced by the PhyloCode.

Successive groups of avialans acquired more and more characteristics of modern birds, including the fusing together of the finger bones in the wing, lengthening the forearm relative to the hind limbs, and shortening of the bony tail. Only a few of these more advanced long-tailed birds are known, including Archie itself, and the Chinese forms *Shenzhouraptor*, *Yandangornis*, and *Dalianraptor*. The most advanced known bird that can reasonably be considered "long-tailed" is *Zhongornis haoae*, which has a very shortened tail, though not as short as *Confuciousornis*, and lacking a pygostyle.[27] Interestingly, it's possible that *Zhongornis* is simply a juvenile *Confuciousornis*, which would have implications for the evolution of short tails: a short-tailed bird that retained a long tail as a chick, almost as tadpoles reduce their tails as they mature into frogs.

Model of the enantiornithan Iberomesornis romerali *at the Museo Nacional de Ciencias Naturales de Madrid. Public domain image from Wikipedia.*

Long-tailed birds and short-tailed birds co-existed during the rapid diversification of birds in the early Cretaceous, but by the end of that period only the descendants of the long-tailed ground birds remained, all flying birds were members of the two primary short-tailed lineages: ribbon-tailed Enantiornithes and fan-tailed Ornithuromorpha. Enantiornithines were the dominant flying birds of the Mesozoic, but all became extinct along with most other dinosaurs. Only a few lineages of Ornithuromorph survived, and these were the Avians, members of the groups that would eventually

produce ducks, fowl, and shorebirds, which diversified into all the modern bird groups during the Cenozoic.

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