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AU:3 **Key words:**

a0005 # LIFE ON EARTH, VERTEBRATES

Contents

AU:1 ## Birds

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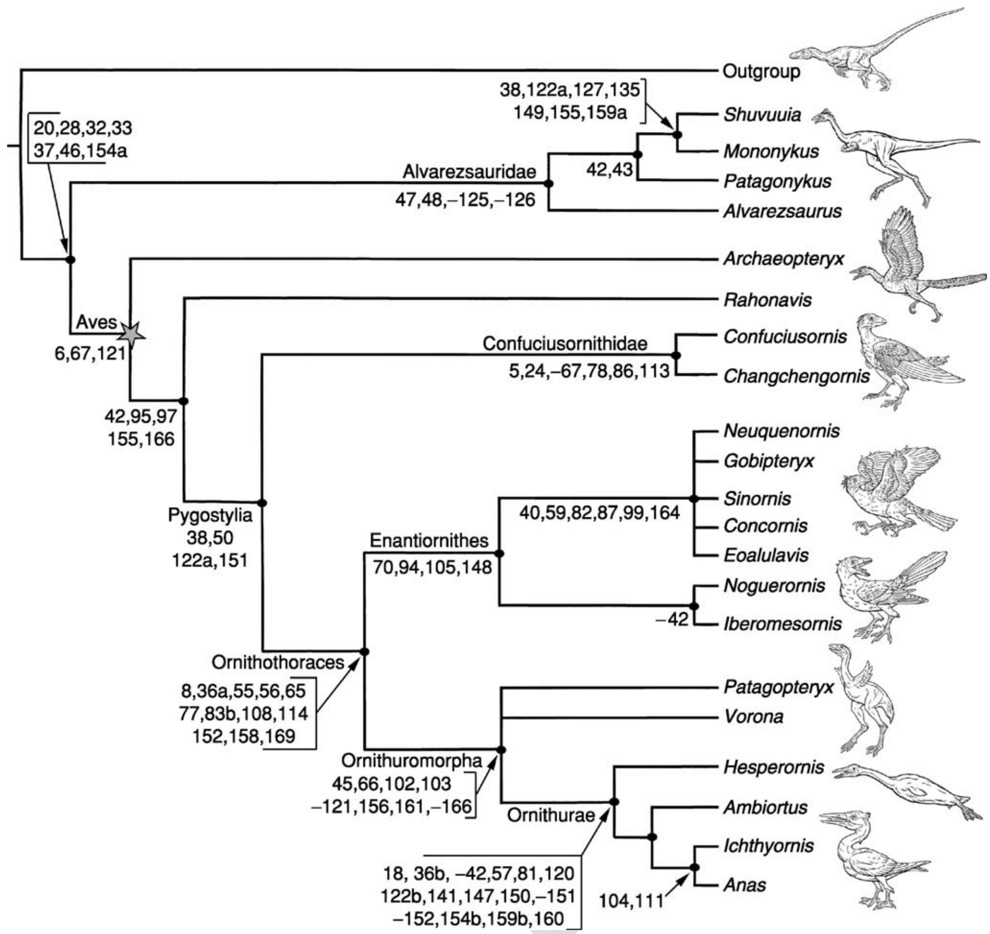
s0005 ### Introduction

p0005 The evolutionary history of birds – class Aves – and their relationships with other groups of fossil and living vertebrates have been debated for more than 100 years. Now, however, the overwhelming consensus among palaeontologists and zoologists is that all living birds and their fossil cousins are the descendants of carnivorous theropod dinosaurs; indeed, evolutionary hypotheses place Aves as a nested group within this subdivision of the dinosaurian family tree (**Figure 1**). As a group, birds are characterized by their active flapping flight and have an almost uninterrupted fossil history from the Late Jurassic (140 Ma) to the Holocene. The earliest phases of their evolution occurred in the Cretaceous, possibly including the origination of modern birds (Neornithes), whose extant orders and families are first recorded in the latest Cretaceous–earliest Tertiary, some 60–70 Ma ago. Throughout the Cenozoic birds radiated (diverged and diversified) to produce the approximately 10 000 species alive today. In this article, we discuss many of the key fossil taxa that have aided our understanding of avian evolution throughout the Mesozoic, outline the geological environments in which they are preserved, and present arguments for the pattern of the evolutionary radiation of modern birds. Although birds are among the most familiar and immediately recognizable of the major living vertebrate groups, very little was known about their early evolutionary history until just a few years ago – recent times have been very exciting for Mesozoic avian palaeontologists: in just the last five years, more fossil bird taxa have been discovered and described from the Cretaceous alone than were known for much of the preceding century.

Birds from the Mesozoic: Not just *Archaeopteryx* s0010

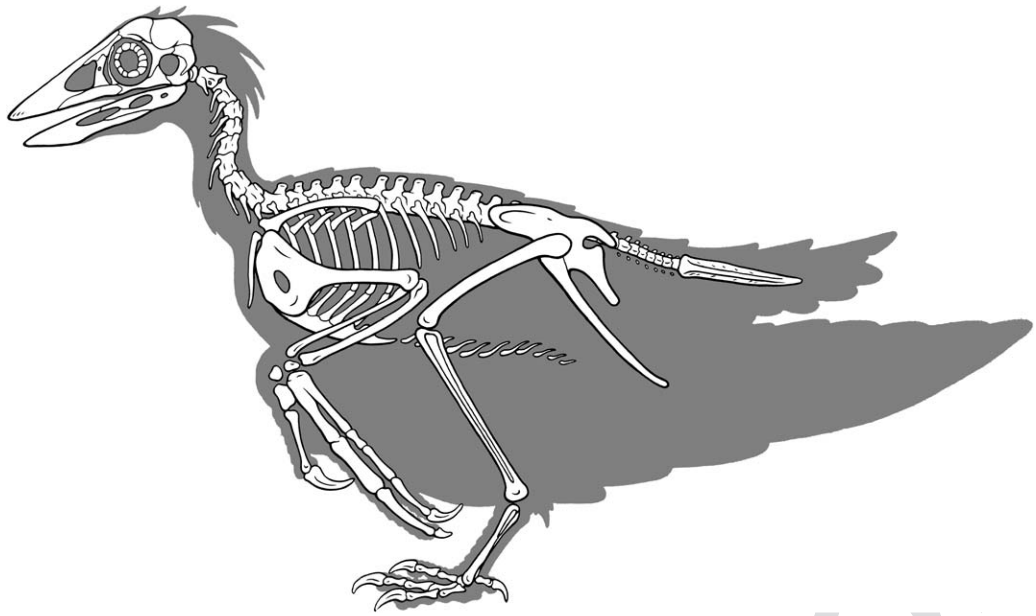
Although it was described nearly 150 years ago from the lagoonal limestones of Solnhofen in Bavaria (Germany), *Archaeopteryx* is still the oldest recognized bird. Eight skeletal specimens and a feather are all that is known of this primitive taxon; all have p0010



AU:8 f0005 AU:9 **Figure 1** Cladogram of Mesozoic bird relationships showing theropod dinosaurs at the base. Many of the taxa seen at the tips of this tree have been described since 1990.

been found in the 140 Ma old Solnhofen limestone deposits, which were formed in a poorly oxygenated hypersaline shallow tropical lagoon, thus facilitating the exquisite preservation of these specimens. A great deal has been written about *Archaeopteryx*. – How well was it able to fly? Was it an arboreal or a terrestrial animal? Do all known specimens come from one or several closely related species? Since its initial description in the 1860s, one thing has remained clear: *Archaeopteryx* provides a tantalizing glimpse of the earliest stages of avian evolution. Having a long bony tail, sharply clawed forelimbs, and a primitive pelvis, this toothed bird is in many ways anatomically more similar to theropod dinosaurs than to today's birds. At one time *Archaeopteryx* was one of very few fossils from the Mesozoic upon which solid evolutionary inferences could be based; however, over the course of the last two decades, more and more fossil information has come to light, revealing an unexpectedly large diversity of primitive birds that existed throughout the last half of the Mesozoic Era. These fossil birds vary vastly in age, degree of preservation, and the environments they inhabited. Although none of these newly discovered lineages have left living descendants, the many exquisite fossils allow us to reconstruct patterns of morphological change, including the origin and development of modern avian wing anatomy. They also furnish evidence documenting the pattern of genealogical relationships of early birds and help us better understand the radiation of extant species.

In addition to *Archaeopteryx*, new fossils that have come to light over the last few years include several of the other most primitive birds known, *Jeholornis* and *Zhenzhoraptor* (which are perhaps synonymous taxa) and *Rahonavis*, from the Early and Late Cretaceous of China and Madagascar, respectively. Although both these taxa retain the long bony tails of *Archaeopteryx* and other non-avian theropods, they show that more advanced shoulder girdles and wings (which characterize more derived birds) had begun to develop by the earliest Cretaceous (*ca*. 125 Ma ago) (**Figure 2**). *Rahonavis* is remarkably theropod-like in its anatomy, even retaining the enlarged sickle claw p0015 AU:4



f0010 **Figure 2** Artist's rendering of *Confuciusornis*, a primitive fossil bird from the Cretaceous of China.

seen on the feet of theropods such as dromaeosaurids. Even though *Rahonavis* is much younger than *Archaeopteryx* (more than 60 Ma younger), the two birds may be closely related.

p0020 Fossil discoveries of birds at the base of the avian evolutionary tree, close in their anatomy to *Archaeopteryx,* have characterized some, but not all, of the advances in the study of avian evolution. Arguably the most significant development in this area came in the early 1980s with the discovery of an entirely new group of Cretaceous birds, the subclass Enantiornithes. More than 20 genera of Enantiornithes have now been discovered and described from all kinds of environments and from throughout the Cretaceous (**Table 1**). It is important to remember, however, that these birds were recognized only in 1981, from the Late Cretaceous of Argentina. The Enantiornithes were by far the most diverse group of Mesozoic birds, showing a good deal of anatomical variation, as well as diversity in their feeding adaptations, flight apparatus, life styles, and patterns of skeletal development. Representatives of this lineage are now particularly well known from the Early Cretaceous of Spain and China. Although most were toothed (e.g. *Sinornis*, *Eocathayornis*, and *Logipteryx*), some did not have teeth (*Gobipteryx*), and they range in size from species that were the size of a sparrow (*Iberomesornis*, *Eoalulavis*) to taxa with wingspans of almost a metre (*Enantiornis*). Their anatomy demonstrates that Enantiornithes were proficient fliers (probably very similar to living birds) and, interestingly, provides some of the earliest evidence for perching (based on the morphology of their feet) that has been found in avian evolution. Although these birds have mostly been recovered from inland deposits, enantiornithines also occupied littoral and marine environments, even extending into the polar regions. Enantiornithes are an anatomically distinctive group (having unique morphological specializations in their forelimbs, hindlimbs, and pectoral girdles) but are not closely related to extant birds (**Figure 1**); these taxa comprise a basal series of lineages that did not survive the end-Cretaceous extinction event.

In addition to these diverse archaic birds, a number of other currently less well-known taxa (in terms of numbers of described fossil specimens) comprise a series of evolutionary intermediates that fits neatly in between the enantiornithine radiation and the divergence of a second major avian group, the Ornithuromorpha (**Figure 1**). Most importantly, this clade contains the immediate relatives of all living birds. Members of the Ornithuromorpha are much more modern in their morphology than are members of the other Mesozoic groups – their earliest records are from the Early Cretaceous of China. Just as in the Enantiornithes, there has been something of an explosion in fossil discoveries of ornithuromorphs in recent years. The exceptionally well-preserved *Apsaravis* from the Late Cretaceous of the Gobi Desert in Mongolia is one example (**Figure 3**). The bulk of the early fossil record of these birds was limited to the flightless loon-like *Hesperornis* and its kin (Hesperornithiformes) and the more modern looking *Ichthyornis* (Ichthyornithiformes) from Late p0025

Table 1 Fossil Mesozoic birds

Taxon	*Stratigraphical age*	*Material*	*Depositional environment*	*Geographical distribution*	*Year described*
Archaeopteryx lithographica	Late Jurassic	Several specimens	Near shore	Germany	1861
Nanantius eos	Early Cretaceous	Single bone	Inland	Australia	1986
Noguerornis gonzalezi	Early Cretaceous	Single specimen	Inland	Spain	1992
Iberomesornis romerali	Early Cretaceous	Single specimen	Inland	Spain	1993
Sinornis santensis	Early Cretaceous	Several specimens	Inland	China	1992
Otogornis genhisi	Early Cretaceous	Single specimen	Inland	China	1992
Boluochia zhengi	Early Cretaceous	Single specimen	Inland	China	1994
Concornis lacustris	Early Cretaceous	Single specimen	Inland	Spain	1995
Eoalulavis hoyasi	Early Cretaceous	Single specimen	Inland	Spain	1992
Protopteryx fengningensis	Early Cretaceous	Single specimen	Inland	China	2000
Archaeovolans repatriatus	Early Cretaceous	Single specimen	Inland	China	2002
Gobipteryx minuta	Late Cretaceous	Several specimens	Inland	Mongolia	1996
Alexornis antecedens	Late Cretaceous	Single specimen	Inland	Mexico	1974
Halimornis thompsoni	Late Cretaceous	Single specimen	Near shore	USA	2001
Enantiornis leali	Late Cretaceous	Several specimens	Inland	Argentina	1976
Eoenantiornis buhleri	Early Cretaceous	Single specimen	Inland	China	1999
Avisaurus archibaldi	Late Cretaceous	Single bone	Inland	USA	1985
Avisaurus gloriae	Late Cretaceous	Single bone	Inland	USA	1995
Soroavisaurus australis	Late Cretaceous	Single bone	Inland	Argentina	1993
Yungavolucris brepidalis	Late Cretaceous	Single bone	Inland	Argentina	1993
Lectavis bretincola	Late Cretaceous	Single bone	Inland	Argentina	1993
Neuquenornis volans	Late Cretaceous	Single specimen	Inland	Argentina	1994
Alvarezsaurus calvoi	Late Cretaceous	Single specimen	Inland	Argentina	1991
Patagonykus puertai	Late Cretaceous	Single specimen	Inland	Argentina	1996
Parvicursor remotus	Late Cretaceous	Single specimen	Inland	Mongolia	1996
Mononykus olecranus	Late Cretaceous	Several specimens	Inland	Mongolia	1993
Shuvuuia deserti	Late Cretaceous	Several specimens	Inland	Mongolia	1998
Enaliornis barretti	Early Cretaceous	Several specimens	Marine	UK	1876
Apsaravis ukaani	Early Cretaceous	Single specimen	Inland	Mongolia	2001
Ambiortus dementjevi	Early Cretaceous	Single specimen	Inland	Mongolia	1982
Gansus yumensis	Early Cretaceous	Isolated postcranial	Near shore	Canada	1997
Hesperornis regalis	Late Cretaceous	Several specimens	Marine	USA	1876
Ichthyornis dispar	Late Cretaceous	Several specimens	Marine	USA	1873
Apatornis celer	Late Cretaceous	Single specimen	Marine	USA	1876
Baptornis advenus	Late Cretaceous	Several specimens	Marine	USA	1876
Parahesperornis alexi	Late Cretaceous	Single specimen	Marine	USA	1989
Chaoyangia beishanensis	Early Cretaceous	Single specimen	Inland	China	1995
Confuciusornis sanctus	Early Cretaceous	Hundreds	Inland	China	1996
Changchengornis hengdaoziensis	Early Cretaceous	Single specimen	Inland	China	1999
Liaoningornis longidigitus	Early Cretaceous	Single specimen	Inland	China	1996
Patagopteryx deferrarisi	Late Cretaceous	Single specimen	Inland	Argentina	1992
Vorona berivotrensis	Late Cretaceous	Single specimen	Inland	Madagascar	1996
Rahonavis ostromi	Late Cretaceous	Single specimen	Inland	Madagascar	1998
Limenavis patagonica	Late Cretaceous	Single specimen	Inland	Argentina	2001
Longipteryx chaoyangensis	Early Cretaceous	Single specimen	Inland	China	2001
Yanornis martini	Early Cretaceous	Single specimen	Inland	China	2001
Yixianornis grabaui	Early Cretaceous	Single specimen	Inland	China	2001

Cretaceous marine sediments in the northern hemisphere. Although much more derived in their anatomy, these birds were described soon after *Archaeopteryx* in the 1870s from rocks formed in the Western Interior Seaway, a shallow tropical sea that bisected North America during the Late Cretaceous. Both are toothed, and *Hesperornis* is known to have been a specialized foot-propelled diver with extremely abbreviated forelimbs (about the size of an emperor penguin), whereas *Ichthyornis* was much smaller and able to fly.

The Radiation of Modern Birds: Bursting into the Cenozoic

Neornithes is the group that includes the 10 000 or so living species of bird. Today, they are a diverse and cosmopolitan group, but their early evolutionary

Color Image

f0015 **Figure 3** The single known specimen of the well-preserved ornithuromorph *Apsaravis* from the Late Cretaceous of the Gobi Desert, Mongolia (reproduced with the kind permission of Mark Norell and the American Museum of Natural History, New York).

history remains far from well understood. Although *Ichthyornis* is the best-known close relative of the Neornithes, several other recently described taxa might be closer. These taxa, however, are known only from extremely fragmentary remains, thus rendering problematic our understanding of their genealogical relationships to the Neornithes. In spite of this, debates have centred on the timing of the origination of the major lineages of Neornithes (the extant orders and families), and specifically on whether or not these taxa differentiated as a group prior to the end-Cretaceous extinction event 65 Ma ago and, if so, how deep does the history of modern birds extend into the Mesozoic?

p0035 Evidence to support or refute hypotheses for the time of divergence of the Neornithes is entirely geological, but the fossil record of putative modern birds from the Cretaceous remains scanty. Just a handful of fossil specimens have been described from before the Createaceous–Tertiary boundary and classified within modern groups; they are mostly single bones that lack clear diagnostic features of extant lineages. It is in the earliest Tertiary that the known fossil record of Neornithes improves dramatically: hundreds of fossils (in many cases complete skeletons, often with feathers and other soft-tissue impressions) are known from a series of localities of Palaeocene and Eocene age (60–55 Ma), particularly in Europe and North America, and from a range

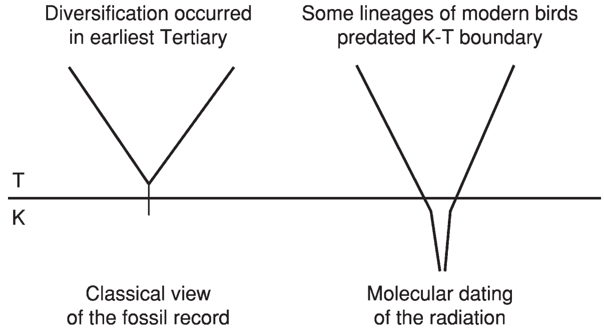


Figure 4 Two competing (alternative) hypotheses for the pattern of the radiation of Neornithes (modern birds). The one on the left is based on fossil data; the one on the right is based on molecular data. f0020

of environments. This abundance of fossil birds that are modern in their anatomy has led some workers to propose that the bulk of their evolutionary radiation occurred rapidly, immediately after the Cretaceous–Tertiary extinction event (**Figure 4**). Related to this, AU:5 there is a further hypothesis that perhaps the extinction itself allowed the repatriation of avian ecological niches that were occupied by more archaic birds during the Cretaceous. These ideas are based on literal readings of the known fossil record of Neornithes – small numbers of taxa (perhaps misidentified) from the Cretaceous, compared with a much larger diversity of definitive Neornithes from the Early Tertiary. Can this approach alone resolve the age-old issue of modern-bird evolutionary dynamics?

Literal interpretations of the fossil record to explain the pattern of the radiation have, however, p0040 been challenged by a number of other lines of evidence, notably the genealogical interpretation of living birds based on genetic data. By considering the numbers of differences in the aligned DNA sequences (both nuclear and mitochrondrial) of living birds and by using either a fossil of known systematic position or a well-dated continental split as a calibration point, new ideas about the timing of the divergence of the major lineages of living birds have been developed, based on the so-called 'molecular clock'. Divergence estimates have been made for a number of groups of living birds and in all cases have indicated that the radiation of the Neornithes occurred much earlier than has been inferred from the known fossil record (**Figure 4**). 'Molecular clock' estimates vary, but have reached a consensus that the majority of the major lineages of living birds did originate sometime in the Cretaceous. It has been argued that these hypotheses, although currently receiving little support from the fossil record, agree with what is known about the pattern of breakup of the continental landmasses during the Mesozoic. A causal correlation between the breakup of landmasses and the differentiation of certain groups of extant birds (i.e. the occurrence of endemic southern-hemisphere taxa towards the base of the neornithine tree) has been proposed, and there is a general agreement among molecular systematists that the initial radiation of the Neornithes probably occurred in the southern hemisphere during the Mesozoic.

p0045 There is thus a discrepancy between the results of studies founded on molecular data and the apparent pattern seen in the fossil record (**Figure 4**). Despite a large number of exceptional fossil-bearing deposits from the Late Cretaceous (especially in the northern hemisphere), convincing remains of modern birds have yet to be found. Opinions about the apparent absence of these birds vary: while some have proposed that it probably reflects a real evolutionary pattern (fossils of other small vertebrates, such as mammals and lizards, are well-known from the Cretaceous), others have suggested that perhaps palaeontologists have not been looking in the right place (relatively little collecting effort has been made in the Cretaceous rocks of the southern hemisphere). What is clear is that the existing records of Cretaceous modern birds should be treated with caution – the earliest neornithine birds that are complete enough to be informative for cladistic analyses, and hence potentially informative for estimating the temporal divergence of the extant lineages, come from rocks that are roughly 55–60 Ma old, deposited some 10 Ma after the end of the Cretaceous.

s0020 Where From Here?

p0050 Thus, palaeontological evidence accumulated over the last decade has cemented the notion that birds are the living descendants of small carnivorous theropod dinosaurs. Exceptional new finds of Cretaceous fossils, especially from China, Spain, Argentina, and Mongolia, have documented a remarkable diversity of avian lineages that thrived and diversified during the latter stages of the Mesozoic. These discoveries have filled substantial anatomical and genealogical gaps in the early history of birds. Yet the evolutionary dynamics (time of divergence and radiation patterns) of the major lineages of extant birds remains an open question that can be resolved only by more well-preserved fossils and a better understanding of their evolutionary relationships.

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