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The Origin and Evolution of Birds

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Abstract

Birds evolved from and are phylogenetically recognized as members of the theropod dinosaurs; their first known member is the Late Jurassic *Archaeopteryx*, now represented by seven skeletons and a feather, and their closest known non-avian relatives are the dromaeosaurid theropods such as *Deinonychus*. Bird flight is widely thought to have evolved from the trees down, but *Archaeopteryx* and its outgroups show no obvious arboreal or tree-climbing characters, and its wing plan form and wing loading do not resemble those of gliders. The ancestors of birds were bipedal, terrestrial, agile, cursorial and carnivorous or omnivorous. Apart from a perching foot and some skeletal fusions, a great many characters that are usually considered 'avian' (e.g. the furcula, the elongated forearm, the laterally flexing wrist and apparently feathers) evolved in non-avian theropods for reasons unrelated to birds or to flight. Soon after *Archaeopteryx*, avian features such as the pygostyle, fusion of the carpometacarpus, and elongated curved pedal claws with a reversed, fully descended and opposable hallux, indicate improved flying ability and arboreal habits. In the further evolution of birds, characters related to the flight apparatus phylogenetically preceded those related to the rest of the skeleton and skull. Mesozoic birds are more diverse and numerous than thought previously and the most diverse known group of Cretaceous birds, the Enantiornithes, was not even recognized until 1981.

The vast majority of Mesozoic bird groups have no Tertiary records: Enantiornithes, Hesperornithi formes, Ichthyornithiformes and several other lineages disappeared by the end of the Cretaceous. By that time, a few Linnean 'Orders' of extant birds had appeared, but none of these taxa belongs to extant 'families', and it is not until the Paleocene or (in most cases) the Eocene that the majority of extant bird 'Orders' are known in the fossil record. There is no evidence for a major or mass extinction of birds at the end of the Cretaceous, nor for a sudden 'bottleneck' in diversity that fostered the early Tertiary origination of living bird 'Orders'.Birds are one of the most recognizable and diverse groups of modern vertebrates. Over the past two decades, a wealth of new fossil discoveries and phylogenetic and macro evolutionary studies has transformed our understanding of how birds originated and became so successful. Birds evolved from theropod dinosaurs during the Jurassic (around 165–150 million years ago) and their classic small, lightweight, feathered, and winged body plan was pieced together gradually over tens of millions of years of evolution rather than in one burst of innovation. Early birds diversified throughout the Jurassic and Cretaceous, becoming capable fliers with supercharged growth rates, but were decimated at the end-Cretaceous extinction alongside their close dinosaurian relatives. After the mass extinction, modern birds (members of the avian crown group) explosively diversified, culminating in more than 10,000 species distributed worldwide today.

Keywords: Birds,Birdsorigen,birdextinctions,flightevolution,evolution,Dinosauria Jurassic, cretaceou

Introduction

Birds are one of the most conspicuous groups of animals in the modern world. They are hugely diverse, with more than 10,000 extant species distributed across the globe, filling a range of ecological niches and ranging in size from the tiny bee hummingbird (~2 grams) to the ostrich (~140,000 grams). Their feathered bodies are optimized for flight, their supercharged growth rates and metabolism stand out among living animals, and their large brains, keen senses, and the abilities of many species to imitate vocalizations and use tools make them some of the most intelligent organisms on the planet(1).

This begs a fascinating question: how did birds achieve such great diversity and evolutionary success? For much of the last two centuries this was a mystery, but over the past two decades a wealth of new fossil discoveries, molecular phylogenetic analyses of living birds, and quantitative macro evolutionary analyses have revolutionized our understanding of bird origins and evolution. This new information reveals a surprising story: birds evolved from dinosaurs and have a deep evolutionary history, during which their signature body plan evolved piecemeal over ~100 million years of steady evolution alongside their dinosaurian forebears before many of the modern groups of birds explosively diversified after the non-avian dinosaurs went extinct 66 million years ago (2,3,4).

Methods

Research Effort Database

Global research effort was estimated for each of the 10 064 bird species listed on the IUCN website (including extinct species) using the Zoological Record database. This database covers over 5,000 serials, plus many other sources of information including books, reports, and meetings, and is thus one of the most exhaustive compilations of the zoological literature. We extracted, for each species, the number of publications referenced in this database between 1978 and 2008 (the extraction was made in June 2012). We used the current Latin names included on the IUCN website as reference names for each species, and searches were made on keywords, abstracts and titles. To test whether this search method could in itself bias our data, we re-estimated research effort on 200 randomly chosen species using article titles only, and compared these estimates with the ones obtained with keywords, abstracts and titles.

As species and genus names are regularly modified with advances in molecular taxonomy, some species are known in the literature by different names, and their research effort is thus likely to be underestimated when only considering the currently used IUCN name. To test for this potential bias, we randomly drew 500 species in the whole class, and collected the different Latin names known for these species on the avibase.com website, an extensive information system containing bird name synonyms. We then re-assessed research effort for these species considering the different Latin names for each of them, and estimated the correlation between this new estimate of research effort and the one based on the current name only. Finally, we tested whether research effort could be biased by taxonomic stability itself, by asking whether the number of different names listed per species was associated with research effort.

Taxonomic prejudice

We first used Phylogenetic Linear Mixed Models (PLMM) with Markov chain Monte Carlo (MCMC) techniques using the R package MCMCglmm to estimate the proportion of variance in research effort (log-transformed) explained by phylogeny. The proportion of variance explained by phylogeny was calculated as the ratio VP/(VP+VR) with VP the variance explained by phylogeny and VR the residual variance. We used the phylogeny from (5) available on http://birdtree.org/. This website does not provide a unique consensus tree, but sample trees from a pseudo-posterior distribution. We randomly extracted 10 different trees, and ran one model per tree, providing 10 phylogenetic and residual variance estimates that we averaged to calculate the proportion of variance explained by phylogeny.

To identify the taxonomic level explaining the most important part of the variance in research effort, we then classified each species by its genus, family, and order, according to the classification used by the IUCN. We used Linear Mixed effects models to estimate the proportion of variance explained by each taxonomic level, using the lme procedure from the nlme R package. Research effort (log-transformed) was used as response variable, and order, family and genus were included as random effects, with genus nested in family, and family nested in order. We compared the AIC of models without any higher taxonomic levels, vs models including only order, vs models with family and order, vs models with genus, family and order. We estimated the proportion of variance explained by each taxonomic level calculating intra-class coefficients (ICC) for each of the 3 taxonomic levels, using variance estimates from the complete model (i.e. with the 3 taxonomic groups). Maximum likelihood was used to compare the AIC for different models, but we used Restricted Maximum Likelihood to get variance estimates used to calculate ICC, as advised in (6).

Geographic prejudice

We tested whether a species biogeographic realm predicted research effort by including biogeographic realm in a linear model with research effort (log-transformed) as the response variable. We used the Biogeographic realms classification from the IUCN, which identifies 13 realms. These data were not available for 4 extinct species, which were excluded from the analysis. We also tested whether insular and continental species had different research efforts, using island and continental status provided on the Birdlife website.

Species Traits prejudice

We tested whether 9 traits often studied in the literature could be associated with research effort. Extinct species (n=134) and species classified as data deficient (n=60) were excluded from these analyses. We first considered the association between research effort and habitat breadth, using habitat data from the IUCN. We expected species inhabiting a larger diversity of habitats to be more easily observable, and thus more often investigated. The IUCN provides a habitat classification scheme that defines 82 different habitat subtypes. Habitats were placed into 8 categories based on the categorization scheme of Bennett and Owens (7): forest; woodland; scrub; tundra, moorland, and mountain; grassland, steppe, savannah, and agricultural; marine; marshland, freshwater habitats; and urban and suburban habitats, and we summed for each species the number of different categories it was recorded in (i.e. from 1 to breeding systems (e.g. brood parasites) to be more often investigated, and migrant species to have higher research effort as migration is a research area *per se*. Finally, as we expected research effort to affect longevity estimates, we considered longevity (available for 8) to obtain our measure of habitat breadth in 9870 species. We also considered distribution range (available for 9758 species; source=Birdlife website) and population size (available for 2945 species; source=Birdlife website) as we expected more widely distributed and abundant species to be more easily investigated. Body mass (available for 7703 species; source: (8) and Birdlife website) was also considered as larger species are more easily observable. Clutch size (available for 4954 species; source: (9), breeding system (available for 9277 species; source: (10) and migratory behavior (binary variable: migrant vs resident species; available for 9875 species; source: Birdlife website) were also considered as we expected species with larger clutches to be important targets in evolutionary studies (especially for studies in quantitative genetics and reproductive biology), species with particular 812 species; source: http://www.demogr.mpg.de/longevityrecords/0303.htm, see also(Table-S2) and generation length (available for 9147 species; source: Birdlife website) in our analyses. For continuous variables, we used Spearman's rho to test for correlations between these traits and research effort, as some of the variables did not follow a normal distribution. A Wilcoxon test was used for the migratory behavior, and a chi-square test for breeding system.

We conducted a second set of analyses using Phylogenetic Linear Mixed Models (PLMM) with Markov chain Monte Carlo (MCMC) techniques using the R package MCMCglmm. These analyses allowed us to test whether phylogenetic biases and species traits biases were confounded, as trait values might not be randomly distributed according to phylogeny. Research effort (log-transformed) was included as response variable, and we included the trait of interest as fixed variable, building one model per trait. We included phylogeny as a random factor, using the phylogeny from(5) available on http://birdtree.org/. We randomly extracted 10 different trees, and ran one model per tree, providing p-values and effects estimates with standard errors showing errors due to phylogenetic uncertainty. Following Hadfield (20), we fixed the covariance structure and used poorly informative priors for the variances. For each model, the MCMC chains were run for 210 001 iterations with a burn-in interval of 10000 to ensure satisfactory convergence. A total of 1000 iterations were sampled to estimate parameters for each model. We checked that autocorrelation levels among samples were lower than 0.1.

Extinction Risk

As research effort prejudice may have strong implications for conservation decisions,we also tested whether species extinction risk was associated with research effort we used the ICCN red list status as our measure of species extinction risk we converted. The risk categories into a binomial. Index with species classified under 'least concern on one side and threatened species on the other'(CR,EN,NT,AND VU,IUCN categories). We. Used a wilcoxon test to compare threatened and least concern species ,extinct(N=132) and species with deficient data in the IUCN database (N=59) were excluded from this analysis.

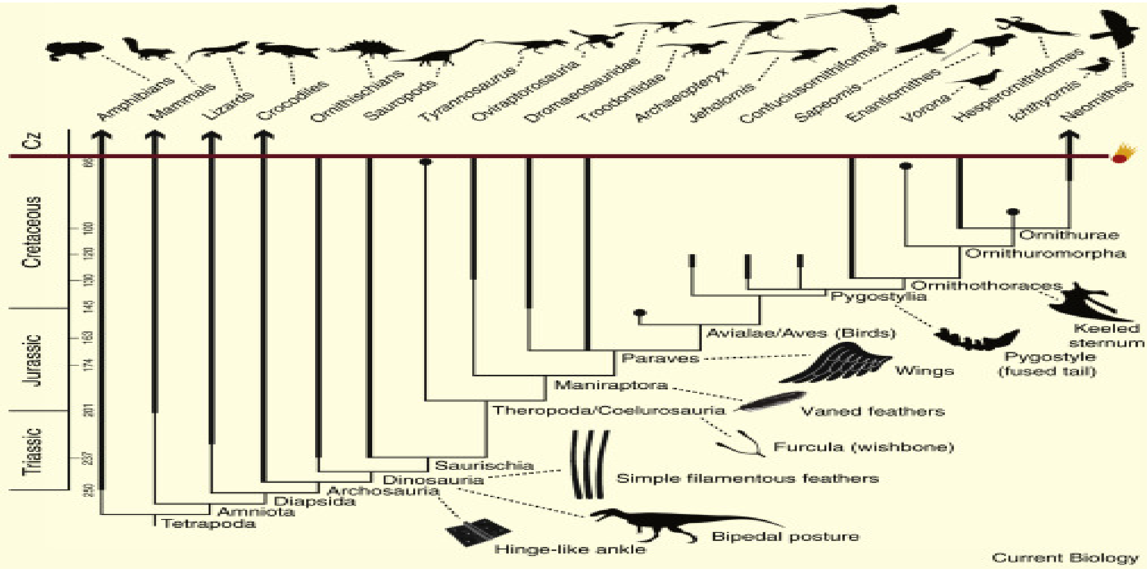

Figure 1. Summary phylogeny (genealogical tree) of birds.

The phylogeny shows where birds fit into the larger vertebrate family tree and the relationships of the earliest birds and their closest dinosaurian relatives (based on (2) and other studies cited therein). Timescale values are in millions of years; thick red line denotes the mass extinction at the Cretaceous–Paleogene boundary caused by asteroid impact (denoted by fireball on the right); arrows denote lineages that survived the extinction; circles represent species known from a particular point in time; thick line sections of branches indicate direct fossil evidence and thin lines are temporal distributions implied by phylogenetic ghost lineages; Cz, Cenozoic interval after the end-Cretaceous extinction. Silhouette anatomical features in the lower part of the figure are plotted approximately where they evolve on the phylogeny. Species silhouettes at the top of the image are from phylopic.org and designed by (from left to right): Nobu Tamura, Anne Claire Fabre, T. Michael Keesey, Steven Traver, Andrew A. Farke, Mathew Wedel, Stephen O'Connor/T. Michael Keesey, Brad McFeeters/T. Michael Keesey, Scott Hartman, T. Michael Keesey, Scott Hartman, Scott Hartman, Matt Martyniuk, Matt Martyniuk, Matt Martyniuk, Matt Martyniuk, Nobu Tamura/T. Michael Keesey, Matt Martyniuk, J.J. Harrison/T. Michael Keesey. 'Bipedal posture' silhouette by Scott Hartman.

The origin of birds is now one of the best understood major transitions in the history of life. It has emerged as a model case for using a combination of data from fossils, living species, genealogies, and numerical analyses to study how entirely new body plans and behaviors originate, and how prominent living groups achieved their diversity over hundreds of millions of years of evolution (2,3). Here, we review what is currently known about the origin, early diversification, and rise to dominance of birds, and the various lines of evidence that piece together this story.

Note that throughout this review, we use the vernacular term 'birds' to refer to a specific group, which is defined in a phylogenetic sense as the most inclusive clade containing *Passer domesticus* (the house sparrow) but not the extinct bird-like dinosaurs *Dromaeosaurus albertensis* or *Troodon formosus*. This clade includes all living birds and extinct taxa, such as *Archaeopteryx* and Enantiornithes. Some researchers refer to this group as Avialae (e.g. 2,5), but others use the name Aves (e.g.6). In this review, we avoid these debates by referring to this group as 'Avialae/Aves' and its members as 'avians'. We use Neornithes to refer to the avian crown group, which comprises all living birds and the descendants from their most recent common ancestor.

The Dinosaur–Bird Link: Once Controversial, Now Mainstream

What did birds evolve from and where do they fit into the family tree of life? For much of the 19th and 20th centuries these questions were hotly debated. The first hint that birds evolved from reptiles appeared in 1861, only a few years after Darwin published *On the Origin of Species*, with the discovery of an exquisite skeleton of a Late Jurassic (ca. 150 million year old) bird from Germany. Named *Archaeopteryx* by British anatomist Richard Owen, this fossil possessed a curious mixture of classic bird features, such as feathers and wings, but also retained sharp claws on the hands, a long bony tail, and other reptilian characteristics(7). Over the next two decades, Thomas Henry Huxley — Owen's great rival and Darwin's most vociferous early supporter — argued that *Archaeopteryx* bore remarkable similarities to small dinosaurs like *Compsognathus*, supporting an evolutionary link between the groups(8,9). This idea gained some acceptance, but fell out of favor during the early 20th century, largely as a result of an influential book by Danish anatomist Gerhard Heilmann(10). Up until the 1960s most scientists held that birds originated from a nebulous ancestral stock of reptiles called 'thecodonts'.

The debate over bird origins was reinvigorated in the 1960s–1980s, as a new generation of paleontologists spearheaded the 'Dinosaur Renaissance'(11). John Ostrom discovered fossils of the astonishingly bird-like dinosaur *Deinonychus* in western North America(12), Robert Bakker and colleagues argued that dinosaurs grew fast and had active metabolisms like living birds(13) and Jacques Gauthier and colleagues used the revolutionary new technique of cladistics to place birds within the family tree of dinosaurs(14) By the 1990s the vast majority of paleontologists accepted the dinosaur–bird link, but many ornithologists remained skeptical. The discovery in the late 1990s in China of fossils from thousands of bona fide dinosaurs covered in feathers provided the most definitive visual evidence for the dinosaur–bird link(15,16,17) convincing most of the remaining skeptics (Figure-2A–C). It is now widely accepted, even by ornithologists, that birds evolved from dinosaurs(18) with the two groups linked by hundreds of shared features of the skeleton, soft tissues, growth, reproduction, and behaviour(2,3,19,21,22) Most amazingly, it is now known that many non-bird dinosaurs were feathered and would have looked much more like birds than lizards or crocodiles(Figure-3).

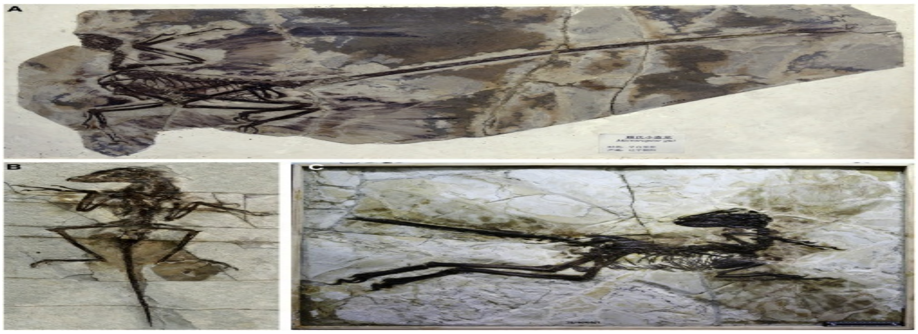

Figure 2. Montage of feathered, bird-like non-avian theropod dinosaurs.

(A) The four-winged dromaeosaurid *Microraptor gui* (photo by Mick Ellison). (B) The small long-armed dromaeosaurid cf. *Sinornithosaurus* (photo by Mick Ellison). (C) The large short-armed dromaeosaurid *Zhenyuanlong suni* (photo by Junchang Lü). All specimens from the Early Cretaceous (130.7–120 million years ago) Jehol Biota of Liaoning Province, China.

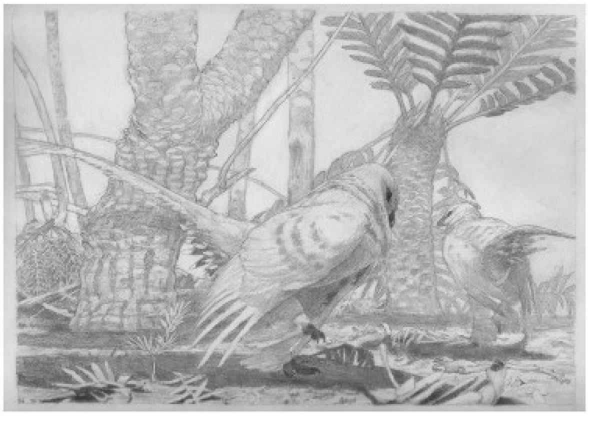

Figure 3. A troodontid dinosaur, one of the closest relatives to birds.

Reconstructed, artistic and scientifically informed appearance of a small troodontid dinosaur and its surrounding environment, illustrating the incredibly bird-like appearance of derived non-avian dinosaurs close to the common ancestor of birds. The male (left) is shown displaying to the female. The environment (Tiaojishan Formation, Middle-Late Jurassic, Liaoning, China) is a seasonally dry woodland dominated by bennettites and cycads. Illustration by Jason Brougham (http://jasonbrougham.com/). Other artistic illustrations and interpretations for these advanced paravian dinosaurs exist in the literature, with various degrees of reptilian and avian features reconstructed, but all depictions are remarkably bird-like.

Where Birds Nest in the Dinosaur Family Tree

Birds evolved from dinosaurs, and therefore are dinosaurs, in the same way that humans are a type of mammal (Figure 1). Birds are nested within the theropod dinosaurs, the major subgroup of mostly carnivorous species that includes the behemoths *Tyrannosaurus* and *Allosaurus*, but also smaller and obviously much more bird-like species such as *Velociraptor*, *Deinonychus*, and *Troodon*(21,22). Birds are members of a nested set of ever-more exclusive theropod subgroups: Coelurosauria, Maniraptora, and Paraves(Figure-1). Their very closest relatives are the mostly small-bodied, feathered, large-brained dromaeosaurids and troodontids, exemplified by the well-known *Velociraptor* (23).

However, the exact relationships among paravians (birds, dromaeosaurids, and troodontids) are uncertain and often vary between competing phylogenetic analyses based on morphological characters, because as more fossils are found it is becoming clear that the earliest birds were very similar anatomically to primitive dromaeosaurids and troodontids, so it is difficult to tell them apart. Thus, there is current debate about whether dromaeosaurids and troodontids form their own clade of close bird relatives, or whether one of them is more closely related to birds than the other(2,5,24). This means that there is also ongoing debate about which fossils are the earliest birds. The iconic *Archaeopteryx* is still widely considered to be among the first birds(2,5,24,25,26) but some studies have suggested that it may instead be a primitive dromaeosaurid or troodontid(27,28). Additional studies have also found other small feathered theropods, such as *Anchiornis* and *Xiaotingia*, to be the earliest birds(24,26), more primitive than *Archaeopteryx*. There is also debate about whether the bizarre, sparrow-to-pigeon-sized, long-fingered scansoriopterygids are basal-most birds or non-bird maniraptorans (2,5,24,25,26,29).These debates will likely continue, but the alternative answers do not change two important points: firstly, that birds first appear in the fossil record during the Middle–Late Jurassic, around 165–150 million years ago (the age of *Archaeopteryx*, *Xiaotingia*, *Anchiornis*, and close dromaeosaurid and troodontid relatives); and secondly, that the oldest birds and their closest relatives were small (roughly chicken-sized), lightweight, long-armed, winged, and feathered animals (Figure-4A,B). The fact that scientists are having a difficult time distinguishing the earliest birds from their closest dinosaur relatives illustrates just how bird-like some non-bird dinosaurs were (Figure-3), and how the transition between non-bird dinosaurs and birds was gradual.

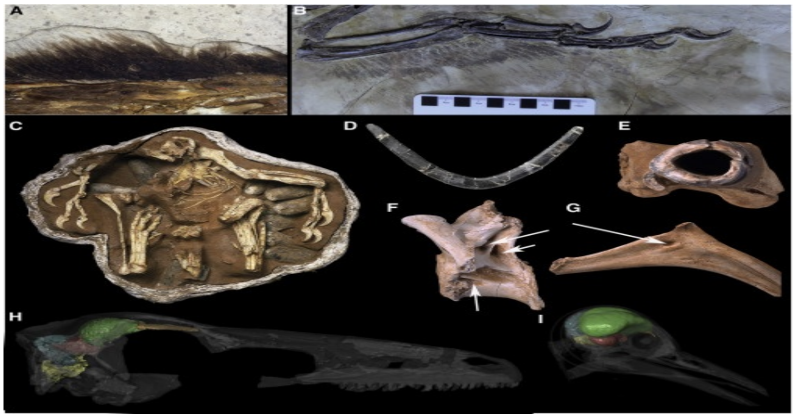

Figure 4. Montage of bird-like features in non-avian theropod dinosaurs.

(A) Simple filament-like 'protofeathers' on the head of the compsognathid *Sinosauropteryx*. (B) Large, branching, vaned feathers forming a wing on the arms of the dromaeosaurid *Zhenyuanlong suni*. (C) Parent oviraptorosaur brooding its nest of large eggs. (D) Furcula (wishbone) of the dromaeosaurid *Bambiraptor feinbergorum*. (E) Hollow internal cavity in the tibia of the tyrannosaurid *Alioramus altai*. (F,G) Pneumatic foramina (denoted by arrows), where air sacs penetrated the bones, in a cervical vertebra (F) and rib (G) of the tyrannosaurid *Alioramus altai*. (H) The reconstructed brain of the troodontid *Zanabazar junior* (orange, olfactory bulb; green, telencephalon; blue, cerebellum; red, midbrain; yellow, hindbrain). (I) The brain of the modern woodpecker *Melanerpes*. Photo in (B) by Junchang Lü; images in (H,I) by Amy Balanoff; all other photos by Mick Ellison.

The Assembly of the Bird Body Plan and Classic Avian Behaviors

The ever-growing fossil record of early birds and their closest dinosaurian relatives, which can be placed in a well-resolved family tree (Figure-1), allow unprecedented insight into how the classic body plan and signature behavioral features of birds originated, evolved, and were related to the phenomenal success of the group (Figure-4). Over the past two decades of research, one overarching pattern has become clear: many features — such as feathers, wishbones, egg brooding, and perhaps even flight — that are seen only in birds among living animals first evolved in the dinosaurian ancestors of birds(Figure-4,5). Other features, such as rapid growth, a keeled sternum, pygostyle, and beak, are absent in the earliest birds and evolved, often multiple times, in more derived birds during the Cretaceous. Therefore, what we think of as the bird 'blueprint' was pieced together gradually over many tens of millions of years of evolution, not during one fell swoop (Figure-1) (2,3,19,20). We describe the assembly of this 'blueprint' below.

Living birds are mostly small and have a highly distinct skeleton well suited for flight. This small body size is a culmination of an evolutionary trend spanning more than 50 million years, beginning in maniraptoran theropods distantly related to birds(40,41,42) The bipedal posture, hinge-like ankle, hollowed bones, and long S-shaped neck of birds were inherited from deep dinosaurian ancestors(43,44), the wishbone (furcula) and three-fingered hands of birds first appeared in primitive theropods, the reversion of the pubis and associated forward movement of the center of mass occurred in maniraptoran theropods, and the ability to fold the forearm against the body evolved in paravians closely related to birds(3,9,20) Other classic avian features, such as the keeled breastbone to support flight muscles and highly reduced tail, evolved after the origin of birds, meaning that the earliest birds looked more like dinosaurs in lacking these features. Long-term trends in skeletal proportions and musculature across dinosaurs and early birds led to two of the most characteristic features of living birds: the elongated arms, which became wings in birds (45), but see(46); and the bizarre 'crouched' hindlimb posture, in which the femur is held nearly horizontal and most of the locomotory activity of the hindlimb occurs at the knee joint rather than the pelvic joint (48).

Perhaps the single most recognizable feature of birds is feathers, which are used to construct an airfoil for flight (the wing), and also for display, thermoregulation, and egg brooding. The evolution of feathers likely began in the earliest dinosaurs, or perhaps even in the closest relatives of dinosaurs(48,49),(Figure-4A,B). A variety of primitive theropods, such as *Sinosauropteryx* and the tyrannosaurs *Dilong* and *Yutyrannus*(17) and a growing number of plant-eating ornithischian dinosaurs, such as *Tianyulong* and *Kulindadromeus* (50,51) are now known from spectacularly preserved fossils covered in simple, hair-like filaments called 'protofeathers' that are widely considered to be the earliest stage of feather evolution(48,52)Elaboration of these structures into the more complex, branching, vaned feathers of modern birds occurred in maniraptoran theropods(48). Some non-bird dinosaurs like *Microraptor* possess feathers basically indistinguishable from the flight feathers of living birds(53,54,55) (Figures 2 and 3) . The story of feather evolution is becoming increasingly clear: the earliest feathers evolved in non-flying dinosaurs, likely for display and/or thermoregulation, and only later were they co-opted into flight structures in the earliest birds and their very closest dinosaurian relatives.

In many derived non-bird dinosaurs, vaned feathers are layered together to form wings on the arms, and in some cases the legs and tails(55,56,57,58,59) Whether these wings were capable of flight, or perhaps used for other functions, such as egg brooding or display(60), is difficult to answer at present, although there is some emerging evidence for multiple uses.

Some non-bird dinosaurs probably did use their wings to fly. Biomechanical study of the four-winged dromaeosaurid *Microraptor* suggests that it was a capable glider, although probably not capable of the kind of muscle-driven powered flight of living birds(61). In further support of *Microraptor*'s volant capabilities, it is the only taxon with asymmetrical hindlimb feathers (flight feathers are asymmetrical with a short and stiff leading vane and are optimized to withstand the force of the airstream), and the only non-avian with an elongated coracoid, a feature of all early birds in which a sternum is present (*Jeholornis*, *Confuciusornis*, and ornithothoracines) (62).

Other non-bird dinosaurs may have used their wings for functions other than flight. Although hindlimb feathers are often regarded as evidence that birds evolved flight through a four-wing stage(58), these feathers are symmetrical (i.e., not well constructed for flight) in all known species other than *Microraptor*. This suggests that their initial purpose was not for flight, but another function, such as display(63). Similarly, a majority of tail morphologies of early birds and close dinosaurian relatives appear to be primarily ornamental in function, suggesting that sexual selection may have been the initial driving force in the evolution of complex paravian plumages, with their use as airfoils for flight coming later(35). A display function for many of these complex feathers would also explain demonstrated increases in melanosome diversity in these dinosaurs, which would have caused the feathers to have a diversity of colors(64).

Therefore, we hold that the following is most likely, based on present evidence. First, much of the evolution of complex feathers and wings in paravian dinosaurs was driven by factors other than flight, such as display. Second, some paravians that evolved flightworthy plumage of large wings composed of asymmetrical feathers (such as *Microraptor* and perhaps other taxa that await discovery) evolved flight in parallel to flight in birds. This latter hypothesis is bolstered by the recent realization that flight probably evolved multiple times within maniraptoran dinosaurs, enabled by structures other than feathered wings: the enigmatic maniraptoran clade Scansoriopterygidae also evolved gliding flight through the use of fleshy patagia similar to flying squirrels(29). If derived bird-like dinosaurs were experimenting with using different body structures to evolve flight in parallel, it follows that different dinosaurs may have evolved different flightworthy feathered wings in parallel as well. Third, although early birds and even some non-bird dinosaurs had volant capabilities, powered flight as we know it in modern birds most certainly developed after the origin of birds themselves.

The earliest birds lacked many key features related to powered flight in modern birds, and probably had primitive flight capabilities that varied substantially between groups. For example, unlike modern birds, *Archaeopteryx* lacked a bony sternum and even a compensatory specialized gastral basket for anchoring large flight muscles(62,65). The slightly more derived *Jeholornis* possessed a curious mixture of features: it retained a primitive long, bony tail unlike that of extant birds, but had several derived flight-related features of modern birds, such as numerous fused sacral vertebrae, an elongated coracoid with a procoracoid process (important in creating the pulley-like system used to minimize effort in the upstroke, otherwise only present in the Ornithuromorpha), a complex sternum, a narrow excavated furcula with a short hypocleidium, and a curved scapula(66,67). *Jeholornis* also had its own peculiarities: it possessed a unique fan-shaped tract of tail flight feathers that likely increased lift and allowed the long tail to be used as a stabilizer, thus producing its own unique and probably very effective form of flight(68).

It was only in birds much more derived than *Archaeopteryx* and *Jeholornis* that the fully modern style of avian flight developed, enabled by a keeled sternum supporting enormous flight muscles, a tail reduced to a fused plough-shaped pygostyle, and a complete triosseal canal in the shoulder (which encloses the pulley-like system that automates the upstroke). These innovations then combined with features evolved earlier in birds and their non-dinosaurian relatives, such as elongation of the feathered forelimbs and a narrow furcula, to produce the style of highly efficient, muscle-driven flight seen in today's birds, which allows some species to fly at altitudes of ~9,000 meters (such as some vultures and geese) and over distances of hundreds of kilometres(1). This modern style of flight developed with or near the origin of Ornithuromorpha. Enantiornithines strongly resemble ornithuromorphs in many anatomical features of the flight apparatus, but a sternal keel was apparently lacking in the most basal members, only a single basal taxon appears to have had a triosseal canal(69), and their robust pygostyle appears to have been unable to support the muscles that control the flight feathers on the tail (retrices) in modern birds (70).

Other distinctive anatomical features of modern birds, relating to the sensory and respiratory systems, first evolved in their dinosaurian ancestors. Living birds are highly intelligent with keen senses, enabled in part by a forebrain that is expanded relative to body size(71). This expansion began early in theropod evolution (72) and non-bird paravians had the highly expanded, and presumably 'flight ready', brain of early birds(73) (Figure-4). Modern birds also possess an efficient 'flow through' lung in which oxygen passes across the gas exchange tissues during inhalation and exhalation, and which is linked to a complex system of balloon-like air sacs that store air outside of the lungs(74). Recent work has surprisingly shown that this system first began to evolve in reptiles, as extant crocodiles and monitor lizards exhibit unidirectional breathing(75,76), but without a complex system of air sacs. The air sacs evolved in early dinosaurs, as shown by the distinctive foramina where the air sacs penetrate into vertebrae and other bones, and became more extensive and elaborate during the course of theropod evolution (77,78,79,,80)(Figure-4F,G). Most theropod dinosaurs at the very least, and possibly other dinosaurs, therefore possessed a 'bird-like' lung.

Extant birds grow remarkably fast, usually maturing from hatchling to adult within a few weeks or months, and have a high-powered endothermic ('warm-blooded') metabolism. As shown by studies of bone histology and growth curves based on counting lines of arrested growth in bones, non-bird dinosaurs grew much faster than previously realized, at a rate intermediate between that of reptiles and modern birds(81,82) . The oldest birds, such as *Archaeopteryx*, and Mesozoic bird groups, such as enantiornithines, had growth rates similar to derived non-bird dinosaurs (83), and the amplified rates and rapid maturation of modern birds probably evolved somewhere around the origin of Ornithurae (3,84).Determining the physiology of dinosaurs is difficult and has been the source of considerable debate for decades (11,13). What is certain, however, is that most dinosaurs had high metabolisms more similar to birds than to living reptiles(85). A recent comprehensive study found that dinosaurs had so-called 'mesothermic' physiologies, intermediate between 'cold-blooded' ectotherms and endotherms (86). The emerging consensus is that the endothermic physiology of living birds had its roots in the mesothermic physiologies of dinosaurs, but was absent in basal birds and developed later in avian history.

The reproductive system of living birds is remarkably derived compared to their closest living relatives (crocodilians) and other vertebrates. Birds possess only a single functional ovary and oviduct and have oocytes that mature rapidly, such that only a single oocyte (or none) is ovulated, shelled, and laid per 24-hour cycle (not numerous eggs en masse as in crocodilians and many dinosaurs). They lay small clutches of large, asymmetrical eggs formed by two or three crystal layers, which typically are actively brooded in the nest by one or both parents(1) (Figure-4). These features evolved incrementally: derived microstructural eggshell characteristics, smaller clutches, and sequential ovulation were acquired in maniraptoran dinosaurs closely related to birds (87,88) . However, derived near-bird dinosaurs apparently retained two functional ovaries (89),whereas *Jeholornis* and enantiornithines apparently had a single ovary, indicating that the left ovary was lost very close to the dinosaur–bird transition, perhaps related to body lightening during the evolution of flight (90). Egg size progressively increased and clutch size decreased during early avian evolution(90).

This summary illustrates how the classic anatomical and behavioral features of birds (the bird ‘blueprint’) did not evolve in one or a few spurts of innovation, but more gradually over a long period of evolutionary time and across the dinosaur family tree (Figure-1). However, there apparently were some bursts of evolution in the early history of birds. Once a small flight-capable dinosaur had been assembled, there was a huge spike in rates of anatomical evolution in the earliest birds (2). Later, the early evolution of short-tailed birds (Pygostylia) in the Cretaceous was associated with high rates of hindlimb evolution and greater than normal speciation(91).

Birds Dealt with a Crisis at the End of the Cretaceous

The course of avian history was dramatically affected by the mass extinction at the end of the Cretaceous, ~66 million years ago, which wiped out all non-avian dinosaurs and many other groups (92,93). The extinction was geologically rapid and most likely caused by the impact of a large asteroid or comet, which triggered a global cataclysm of climate and temperature change, acid rain, earthquakes, tsunamis, and wildfires (94,95). It is possible that somewhat longer-term changes in the Earth system, including volcanism and sea-level fluctuations, may have also played a role in the extinction (96). The emerging picture, however, is that the world changed suddenly at the end of the Cretaceous, killing off many once-dominant groups and giving other organisms an opportunity to radiate in the vacant ecospace.

Birds were diverse in the Late Cretaceous, with many of the characteristic lineages of ‘archaic’ birds from the Jehol Biota (species outside of the neornithine crown, such as enantiornithines and basal ornithuromorphs) living alongside what was probably a moderate diversity of early neornithines, as indicated by rare fossils and molecular phylogenetic studies tracing some modern lineages into the Cretaceous (4,39,97,98). None of these ‘archaic’ non-neornithine birds, however, apparently survived past the Cretaceous and into the Paleogene. There has long been debate about whether the extinction of ‘archaic’ birds was gradual or sudden, but recent evidence shows that a diverse avifauna of enantiornithines and basal ornithuromorphs persisted until at least a few hundred thousand years before the end of the Cretaceous in western North America, suggesting that the extinction was sudden and directly linked to the end-Cretaceous impact (99). This also indicates that birds were strongly affected by the end-Cretaceous extinction, with many major early groups going extinct, countering the stereotype that the mass extinction decimated the non-avian dinosaurs but largely spared birds (see reviews in (92,99). However, because of the scrappy fossil record of the latest Cretaceous birds, which is mostly limited to isolated bones (99), it has been unclear why certain birds went extinct and others survived.

Multiple lineages of early neornithines must have endured the extinction, leaving them the only surviving members of the initial Mesozoic radiation of birds. Fossil (100,101) and recent genetic (4) evidence supports this view and shows that these birds diversified rapidly in the post-apocalyptic world, probably taking advantage of the ecological release afforded by the extinction of both the 'archaic' birds and the very bird-like non-avian dinosaurs. Numerous groups of modern neornithines make their first appearance in the fossil record during the ~10 million years after the end-Cretaceous extinction (102), and a genome-scale molecular phylogeny indicates that nearly all modern ordinal lineages formed within 15 million years after the extinction(4), suggesting a particularly rapid period of both genetic evolution and the formation of new species(Figure-6). We discuss this recent phylogenomic st

Birds after the Cretace

The phylogenetic relationships of Neoaves have been the subject of extensive work in recent years. The recent phylogenomic study by Jarvis *et al.* (4) is the most comprehensive genome-scale analysis of birds to date in terms of amount of DNA sequence (using up to ~300 million nucleotides) and number of analyses, and attempted to resolve two main issues: firstly, the general branching patterns between the major orders on the bird family tree; and secondly, when these groups diverged, particularly which groups originated before the end-Cretaceous extinction and which arose afterwards. The study was able to resolve, with the highest level of certainty to date, the ordinal relationships of modern birds, and determine that the majority of these groups diverged immediately after the Chicxulub asteroid impact that ushered out the Cretaceous.

According to the dated phylogeny of Jarvis *et al.* (4), the common ancestor of Neoaves lived in the Cretaceous. The earliest divergence of this ancestor gave rise to the major subgroups Columbea (consisting of doves, flamingoes, grebes, and sandgrouse) and Passerea (consisting of all other neoavian species). We predict that this ancestor may have been ecologically similar to modern shorebirds, since the number of divergences after the Columbea and Passerea split, and thereby also after the Neognathae split, to obtain an aquatic or semi-aquatic versus terrestrial species are almost equal (Figure -6) (4).

At least four to six of these basal Neoaves lineages and several members of Palaeognathae and Galloanseres are predicted to have passed through the end-Cretaceous extinction. The subsequent burst of speciation after the extinction consisted of an initial rapid radiation of additional basal Neoaves orders, from grebes to hummingbirds, followed by two subsequent radiations of 'core waterbirds' (including penguins, pelicans, and loons) and 'core landbirds' (including birds of prey, woodpeckers, parrots, and songbirds). As mentioned above, nearly all of these ordinal divergences occurred within the first 15 million years after the mass extinction, with this pulse of evolution ending around 50 million years ago.

In general, the results of the Jarvis *et al.* (4) study are consistent with earlier studies proposing a major post-Cretaceous radiation of birds (99,104)and the hypothesis that shorebird-type species were able to endure the extinction (100,101) with traits that may have allowed them to live in diverse environments. However, these new results are at odds with previous molecular studies suggesting a major pre-Cretaceous divergence of Neoaves 20–100 million years earlier (97,105,106) The main differences with some previous molecular studies are that the Jarvis *et al.* (4) study used genomic-scale data and took a conservative approach of using non-ambiguous fossils for dating the tree. In sum, the new phylogenomic study supports a 'short fuse' hypothesis for modern bird diversity (e.g.(100) , in which some of the main extant lineages originated during the final few tens of millions of years of the Cretaceous, but the key interval of speciation and ordinal-level diversification was concentrated in the few million years after the end-Cretaceous extinction.

The new phylogenetic analysis revealed some surprising relationships among well-known living birds, which help to better understand the evolution of important anatomical and ecological traits. Among the Columbea, the flamingos and grebes (both waterbird orders) were found to be sister clades(107) and their closest relatives were inferred to be a landbird group consisting of pigeons, sandgrouse, and mesites (Figure 6). This suggests that the aquatic or terrestrial adaptations of these groups with the 'core' waterbirds and landbirds are convergent. Among the 'core' waterbird group, there appears to be a graded acquisition of aquatic traits, beginning with the sunbittern/tropicbird clade and culminating in penguins and pelicans amongst others, which are more obligate water-dwellers.

The common ancestor of the 'core' landbirds was inferred to be an apex predator, closely related to the extinct giant terror birds (Phorusrhacidae) that included human-sized apex predators in North and South America during much of the Cenozoic (around 62–2 million years ago) (107,108).The species at the deepest branches of 'core' landbirds (vultures/eagles/owls and seriemas/falcons) are predatory, but within this group the raptorial trait appears to have been lost twice: once among the Afroaves clade, on the branch leading to Coraciimorphae (mousebirds to bee eaters), and again among the Australaves clade, on the branch leading to Passerimorphae (parrots to songbirds) (Figure-4). The names of Afroaves and Australaves imply their likely geographical origins(109), although more evidence is needed to confirm this. One interpretation of such independent losses of the raptorial trait is that being a predator is a costly lifestyle for modern birds and is being selected against over time. Another interpretation is that this trait was passively lost twice.

The new phylogeny also helps to better understand the evolution of one of the most intriguing traits of some living birds: vocal learning, including the ability of some species to imitate human speech. This is a very rare trait, seen in only in songbirds, parrots, and hummingbirds among birds and very few mammals (e.g. dolphins, bats, elephants, and humans) but not non-human primates. As such, avian vocal learners have become highly studied animal models of human speech(110,111,112).In contrast to long-standing inferences of three independent gains(103,110,113) the new analysis supports two independent gains of vocal learning amongst Neoaves: once in the hummingbirds and once in the common ancestor of parrots and songbirds, followed by two subsequent losses in New Zealand wrens and suboscines. However, it does not completely rule out independent evolution in parrots and songbirds (Figure-6) (4) . All three vocal-learning bird lineages and humans were found to have evolved convergent mutations and changes in gene expression in the regions of the brain that control song (bird) and speech (human)(98,114) . Overall, these findings reveal the great amount of diversity and convergence that occurred among birds (including some features convergent with mammals) during the post-Cretaceous revolution.

Conclusions

This study provides strong evidence for the nocturnality of the diapsid lineages, paralleling that of the synapsid lineages. Given their nocturnality, an integrated perspective on the evolution of BMSC as a convergent adaptation to nocturnality is proposed. Moreover, after summarizing our findings and relevant empirical studies on the evolution of endothermy, low temperature is suggested as a possible common factor underlying endothermy evolution in vertebrates. Given the significance of low temperature in endothermy evolution, a conceptually unifying ecological model of endothermy evolution with an emphasis on low temperature is proposed. We reason that endothermy may evolve as an adaptive strategy to enable organisms to effectively implement various life-cycle activities under relatively low-temperature environments, which happens during a habitat shift from a high-temperature environment to a relatively low-temperature environment.

Modern birds achieved their enormous diversity over a more than 150 million year evolutionary journey, which began with their divergence from theropod dinosaurs, continued with the gradual and piecemeal acquisition of a flight-worthy body plan, and involved two bursts of diversification: first in the Mesozoic when a small, feathered, winged dinosaur was fully assembled, and second when surviving species had the freedom to thrive after the end-Cretaceous extinction. The origin of avian diversity reveals some greater truths about evolution over long timescales, namely that major living groups have a deep history, underwent long and often unpredictable paths of evolution, and were given unexpected opportunities to radiate if they were able to survive mass extinctions that decimated other groups. The flurry of recent work on avian evolution is a prime example of how fossil, morphological, genomic, phylogenetic, and statistical data can be combined to weave an evolutionary narrative, and explain how some of the modern world's most familiar species became so successful.

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