A new time tree reveals Earth history’s imprint on the evolution of modern birds

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Determining the timing of diversification of modern birds has been difficult. We combined DNA sequences of clock-like genes for most avian families with 130 fossil birds to generate a new time tree for Neornithes and investigated their biogeographic and diversification dynamics. We found that the most recent common ancestor of modern birds inhabited South America around 95 million years ago, but it was not until the Cretaceous–Paleogene transition (66 million years ago) that Neornithes began to diversify rapidly around the world. Birds used two main dispersion routes: reaching the Old World through North America, and reaching Australia and Zealandia through Antarctica. Net diversification rates increased during periods of global cooling, suggesting that fragmentation of tropical biomes stimulated speciation. Thus, we found pervasive evidence that avian evolution has been influenced by plate tectonics and environmental change, two basic features of Earth’s dynamics.

INTRODUCTION

Modern birds (Neornithes) are the most diverse group of terrestrial vertebrates in terms of their species richness and global distribution, yet we still have a poor understanding of their large-scale evolutionary history. Major advances in our knowledge of phylogenetic relationships have been made over the last decade (1–4), but the lack of a robust time tree, along with a comprehensive quantitative biogeographic analysis, has hindered progress toward a better understanding of the process of diversification in modern birds.

Determining the timing of avian diversification has been difficult. There is now a broad agreement that modern birds originated sometime in the Cretaceous (3, 5–8), but actual molecular age estimates vary from 72 mega-annum (Ma) (4) to 170 Ma (5), and fossils of indisputable neornithine affinities have only been found in the latest Cretaceous, about 67 Ma ago (9). Similarly, there is no agreement on the timing of diversification within the three major avian groups: Palaeognathae (tinamous and ratites), Galloanseres (waterfowl, pheasants, and allies), and the megadiverse Neavises (all other birds); whereas most molecular estimates date the early radiation within these groups before the Cretaceous–Paleogene (K-Pg) transition (5, 7, 10–14), with very few exceptions fossils have been found only after the K-Pg extinction event (6, 15–17). The possibility of a rapid post-K-Pg radiation of birds has led some to suggest a major effect of ecological opportunity on avian diversification due to the extinction of major competitors [the “big bang” model (13, 15)]. The big-bang model of avian diversification has received renewed attention because some recent molecular time trees recovered the rapid radiation of Neavises as coinciding with the K-Pg event (3–5, 7); among them, time trees inferred using genomic data represent an important advancement because they overcame several drawbacks of previous analyses by using hundreds of loci and 19 fossil calibrations in Bayesian relaxed-clock analyses (3, 4). Previous estimates suffered from difficulties in modeling molecular evolution, due to reliance on few or misleading fossils or biogeographic events, or limitations of the analytical techniques available (7, 8). However, these genomic time trees depended on priors that restricted the maximum age of the tree based on expert opinion, and changing these priors changed the resultant time tree and the rapid radiation of Neoaves relative to the K-Pg event (19, 20).

Intertwined with questions about the temporal history of birds are those about their biogeographic history; in particular, did Gondwanan paleogeography play a significant role in their early diversification, and what historical events were associated with modern birds becoming globally distributed? With the broad acceptance of plate tectonics and the rise of phylogenetic thinking, it was proposed that multiple groups of birds arose on one or more Gondwanan continents (21–23). Although it is now widely acknowledged that some clades of birds, such as Passeriformes, are southern in origin (24, 25), the extensive Paleogene fossil record in the Northern Hemisphere is often interpreted as being in conflict with the southern origin of many, if not most, groups (15, 18, 26, 27). Biogeographic history also has important implications for the estimation of time trees. For example, the absence of fossil Neornithes in the Late Cretaceous Niobrara formation of North America has been used to constrain the maximum age of this clade (4), but if Neornithes originated on a different continent, this calibration may underestimate its age.

Here, we present a new estimate of the global avian time tree using an empirical approach to determine calibration priors. We also took advantage of recent advances in our understanding of phylogenetic relationships among extant (3, 28) and fossil (6, 29, 30) birds and used slowly evolving nuclear genes amenable to more tractable models of molecular evolution (3). The time tree is then used to explore spatial and temporal patterns of global avian diversification.

RESULTS AND DISCUSSION

A new time tree for birds

We identified avian clades that have a relatively old and well-characterized fossil whose affinities are well established by phylogenetic analysis and/or derived morphologies. These fossils set a minimum bound for the stem age of the corresponding clade and its sister group (Fig. 1A) (31–33). However, phylogenetic divergence time estimation also requires constraints on the maximum age of clades; otherwise, an arbitrarily old tree would be compatible with any minimum bound. Maximum age
constraints can be based on the absence of fossils in earlier fossiliferous beds, but the absence may reflect fossilization and recovery biases rather than true absence. For example, even if a detailed fossil record suggests the absence of a clade in the Paleocene of Europe, the clade may have originated earlier in another less-studied region such as South America. Fossil recovery biases can be quantified and incorporated into age estimates (34, 35) but not without theoretical and practical difficulties (32, 33). This problem is exacerbated by methods that constrain clade age based on maximum bounds (36–38) because bounds do not reflect the uncertainty associated with maximum age constraints. A better approach is to use probability density functions as priors in Bayesian analyses (32, 39), but choosing among different functions and the parameters of those functions has been a subjective and contentious issue (33, 40).

Here, we overcame these problems by empirically generating calibration priors based on the fossil record. We modeled clade age uncertainty based on distributions of fossils finds. A set of fossil ages \( t_1, ..., t_n \) represents a sample from a distribution that has a maximum bound \( \theta \), which is the age of the clade. The objective is to obtain a probability distribution for the age \( \theta \). Several methods have been developed to estimate the stratigraphic range of taxa from observed fossil ages either by assuming simple distributions of fossil ages (41, 42) or by modeling fossil recovery potentials (34). In the simplest case, when fossil ages \( t_1, ..., t_n \) are uniformly distributed, the likelihood of a hypothesized age \( \theta \) is simply \( 1/\theta^n \) for \( \theta > t_n \) (41, 43), and in the absence of prior information, this likelihood is proportional to the probability of \( \theta \) (43).

An important factor that should be taken into account is the geographic dimension of the fossil record, which includes not only fossilization and exhumation biases but also the vagaries of dispersal and colonization processes. For example, a clade may have a temporally dense fossil record in a region including the oldest fossil of the clade worldwide; in a naïve assessment, this would suggest that the clade originated shortly before the age of its oldest fossil. However, if the clade originated in a different geographic region, this age estimate would correspond to the age of dispersion into the region, not the age of the clade. We minimized this problem by analyzing the fossil record at a large geographic scale using only the first fossil occurrence of a clade in each continent. Therefore, for each avian clade with a well-characterized fossil record, we determined the oldest fossil on each continent through bibliographic and database searches and kept only those clades whose set of ages do not depart from a uniform distribution (data set 1; table S1). We then parameterized probability density functions such that they matched the shape of the likelihood functions (fig. S1) and used them as clade age priors in Bayesian divergence time estimation (table S1; further details and extensions are explained in Fig. 1 and Materials and Methods).

We used the empirical priors derived above in Bayesian divergence time estimation in the program BEAST 2 (44), using a genomic data set of 1156 clock-like exons for 48 species from Jarvis et al. (3) and a data set with a much denser taxonomic representation of recombination-activating genes (RAG-1 and RAG-2) for 230 species representing 202 families and all avian orders. Both data sets resulted in very similar estimates of the avian time tree. Both placed the most recent common ancestor of extant birds in the early Late Cretaceous, with the genomic data set resulting in slightly older ages [median, 96.6 Ma; 95% highest posterior density (HPD), 84.2 to 114.3 Ma; Fig. 2A] than the RAG data set (median, 91.5 Ma; 95% HPD, 79.8 to 106.8 Ma; Fig. 2B). These estimates for the crown age of Neornithes are younger than
Fig. 2. Time trees of modern birds from Bayesian divergence time estimation using fossil calibrations. Maximum clade credibility (MCC) trees from a Bayesian divergence time estimation using calibration priors inferred from the fossil record. (A) MCC tree from the analysis of 124,196 bases from the first and second codon positions of 1156 clock-like genes from Jarvis et al. (3) and 10 calibration priors. (B) MCC tree from the analysis of 4092 bases of the recombination-activating genes for 230 species and 24 calibration priors. Black diamonds are calibration nodes, black dots are clades that were constrained to match relationships supported by recent multilocus and genomic analyses (3, 28), red density distributions are clade age prior probabilities derived empirically from a quantitative analysis of the fossil record of clades, and blue bars represent 95% highest posterior densities for node age from the posterior distribution. Median ages are indicated for large clades mentioned in the text (blue dots).
most previous estimates (5, 10–12), but higher posterior densities overlap with the recent analysis of bird genomes (3), in which a maximum age constraint was assumed for the age of Neornithes at the Early-Late Cretaceous boundary. Our analysis recovered a relatively young age for Neornithes without prior constraints on its age.

Radiation within the three major clades—Palaeognathae, Gallonseres, and Neoaves—began around the K-Pg transition (Fig. 2). Initial cladogenesis in Gallonseres and Neoaves occurred just before the K-Pg transition, whereas the timing of initial cladogenesis in Palaeognathae is poorly constrained and spans pre- and post-K-Pg times (Fig. 2). Overall, it is possible that initial radiation of these three major crown clades occurred more or less simultaneously around (and probably before) the K-Pg event, thus suggesting common causal factors. All avian orders originated during the Paleocene (median stem age; Fig. 2), except for Anseriformes and Galliformes, which originated in the latest Cretaceous, and some orders within the higher ratites, which may have originated in the late Paleocene or early Eocene, taking into account uncertainty.

Large-scale biogeographic history of birds

Next, we integrate phylogenetic relationships and the avian time tree with the spatial history of the major lineages of birds, set in the context of paleogeography and paleoclimatology. Because biogeographic history is far too complex to be inferred from ancestral reconstructions alone, our interpretations of the spatial history of birds are also derived from the joint geographic and temporal history among deep stem lineages (that is, avifaunas), the fossil record, phylogenetic and biogeographic patterns within clades, and how those data can be reconciled with Earth history.

We identified the geographic origin of Neornithes and of its three major subclades (Palaeognathae, Gallonseres, and Neoaves) to be West Gondwana, here taken to encompass a united continental South America, West Antarctica, and portions of East Antarctica (Fig. 3). This conclusion is robust to methodological assumptions (parsimony versus probabilistic modeling) and alternative tree topologies, with the exception that the likelihood reconstruction for the most recent common ancestor of Palaeognathae is ambiguous and includes both West Gondwana and the Palearctic (fig. S3). In addition to these basal groups, we reconstructed 22 major groups of Neornithes as being present in South America by the end of the middle Paleocene (~59.2 Ma) (Fig. 3 and table S2). The exact configuration of the land connection between South America and West Antarctica is uncertain, but this terrestrial corridor was potentially disrupted as early as ~50 Ma to as late as ~40 to 37 Ma, when a deep opening of the Drake Passage is inferred (53–56). Continental blocks comprising the corridor would have remained in proximity until ~30 Ma (55, 57).

Before ~83 Ma, Zealandia was conjugate to the eastern Australian margin and to West Antarctica in the south (58, 59). At that time, sea-floor spreading began in the Tasman Basin and south of the Campbell Plateau, severing a direct connection between Zealandia and West Antarctica, thus establishing the Tasman Gateway as the primary corridor for a K-Pg biota to enter Australia and then Zealandia (59). The South Tasman Rise did not rift from East Antarctica until the middle to late Eocene ~40 to 33 Ma; before then, the continental fragments comprising the South Tasman Rise were intermittently subaerial and shallow marine, with terrigenous sedimentation persisting through the Eocene (60, 61). Our results suggest that at least seven to nine major clades involving palaeognaths, Gallonseres, crocimulgiforms, and psittacopasserines (parrots and passerines) were shared with Australia before its separation from Antarctica (table S2). Two additional lineages, tree swifts (Hemiprocnidae; 95% HPD, 21.4 to 43.1 Ma) and the Kagu (Rhynochetidae) (95% HPD, 16.9 to 45.2 Ma), may have also been part of this interchange, considering age uncertainties. Previously, biogeographers had assumed that the ~83-Ma split between Zealandia and West Antarctica and the initial formation of the Tasman Sea implied that younger elements of the biota must have arisen via long-distance dispersal (23), but this assumption of a deep age for the Zealandia biota is no longer necessary (59). Rather, biogeographic patterns of deeper avian lineages were likely established by multiple episodes of vicariance within an early Tertiary biota that occupied Australia and emergent portions of Zealandia (table S2). The presence in Zealandia of two ancient lineages of flightless palaeognaths (kiwis and moas) [the flightless Kagu on New Caledonia and its flightless sister group (Aptornis) on New Zealand], as well as ancient lineages of parrots and passerines, is consistent with this interpretation.

We hypothesize that Neornithes spread from West Gondwana to the rest of the world via two principal routes. The first route is a trans-Antarctic corridor that linked West Gondwana to Australia and Zealandia during the Cretaceous and early Paleogene (Fig. 3) (44). This corridor enabled the establishment of a widespread southern biota with a diversity of organisms, including plants (50), dinosaurs (51), mammals (52), and birds (Fig. 3 and table S2). The exact configuration of the land connection between South America and West Antarctica is uncertain, but this terrestrial corridor was potentially disrupted as early as ~50 Ma to as late as ~40 to 37 Ma, when a deep opening of the Drake Passage is inferred (53–56). Continental blocks comprising the corridor would have remained in proximity until ~30 Ma (55, 57).

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We propose that there was a second Paleogene gateway for avifaunal expansion out of West Gondwana involving North America (here termed the North American Gateway hypothesis). Although it has long been assumed that there was a wide ocean barrier between South and Middle America through the Late Cretaceous and Paleogene until the Plio-Pleistocene, we hypothesize a northward avifaunal expansion at this time coincident with the first appearances of Laurasian metatherian and placental mammals in South America (45, 62), thus implying the presence of a land bridge. Although the paleogeographic setting of lower Middle America is complex and controversial, this interpretation is consistent with a growing number of tectonic models that posit a southern land bridge (63–65) that resulted from subduction, arc magnetism, and collisionary processes involving movement of the Galapagos large igneous province into the Caribbean, spanning K-Pg times.

Our results suggest a central role for North America as a gateway for biotic dispersion into the Holarctic, especially during the Paleocene to early/middle Eocene. Northern Hemisphere Paleogene environments
Fig. 3. Time tree of modern birds with reconstruction of ancestral geographic regions. Fitch parsimony optimizations of ancestral geographic regions are shown at the nodes. Multiple regions at a node represent alternative, equally parsimonious optimizations. The tree is the maximum clade credibility tree of a Bayesian analysis of recombination-activating genes for 230 species and 24 calibration priors and with the addition a posteriori of 25 fossil taxa that represent Holarctic distributions for clades now restricted to the tropics. Distributions at the tips are those of the clades they represent. Schematic representations of global paleogeography at the K-Pg transition, the middle Eocene, and the middle Miocene are shown together with major postulated interregional connections as inferred from paleogeographic evidence and biogeographic analysis. Higher-level taxa are indicated on the right (see fig. S2 for species names).
were broadly tropical and subtropical at lower latitudes and subtropical-warm temperate at higher latitudes, especially toward the Paleocene-Eocene Thermal Maximum (66–69). We infer that these avifaunas diversified within the Nearctic and spread into the Palearctic by the end of the Paleocene and earliest Eocene ~56 to 53 Ma (Fig. 3 and table S2).

The biogeographic analyses suggest that North America played a formative role in the origins of lineages that subsequently diversified in the Old World. Thus, the Green River Formation (53 to 51 Ma) (70) in North America and the Fur Formation (55 to 54 Ma) (71) and Messel oil shales (47 Ma) (29) in Europe record many of the stem lineages that were elements of a widely distributed Paleogene avifauna (table S2). The time tree is consistent with these lineages having initiated diversification before deposition of these fossils. For example, instead of the Coraciiformes arising in Africa (72), our optimizations indicate that Leptosomatiformes, Coliiformes, and Coraciiformes colonized the Paleotropics independently from North American ancestors (Fig. 3). Given the presence of many of these lineages in the early Paleogene of Europe, we infer that they reached the western Palearctic through a North Atlantic corridor before ~52 Ma (table S2). The tectonic history of the North Atlantic in the Paleogene indicates land connections among northeastern North America, Greenland, and Europe (73, 74), and paleontological evidence records mammalian faunal interchange until sometime in the early Eocene (68, 75), when sea-floor spreading between northeastern Greenland and Europe would have created an ocean barrier ~53 to 52 Ma (73, 76).

Expansion into other Old World landmasses is more difficult to circumscribe temporally and geographically. The avian Paleogene record for Africa is sparse, and that for Madagascar is lacking entirely (29). Some old stem clades now characteristic of these two land masses are found in the North American or European fossil record (29). Both Malagasy endemic cuckoo rollers (Leptosomatiformes) and true rollers (Coracioidae) have Holartic Paleogene records, but when they did arrive in Africa or Madagascar is unclear. Our reconstructions suggest that lineages arrived in Madagascar in the Paleocene (mesites, Mesitornithidae), the Eocene (ground rollers, Brachypteraciidae), and the Oligocene (vangas, Vangidae; Fig. 3), suggesting that the buildup of the Malagasy endemic avifauna may have been a protracted process that spanned at least the entire Paleogene.

A second route from North America to the Old World—the Bering land bridge—would have been emergent over much of the Tertiary and, depending on eustatic sea levels and high-latitude temperature gradients, would have facilitated frequent biotic interchange between Asia and North America (77, 78). However, a Beringian corridor for Paleogene avifaunas is not evident in our analysis, partly as a result of a poor fossil record in northern Asia. Cranes and their allies (Gruiformes) provide an exception, with Eocene-Oligocene fossil families Geranoididae in North America and Eogruidae in Asia showing close affinities (29). Several other stem lineages associated with the North Atlantic corridor may also have had Paleogene histories across Beringia, including stem-Struthioniformes (ostriches) and Caprimulgiformes such as frogmouths (Podargidae) and swifts (Apodidae) (Supplementary Materials).

A novel implication of the North American Gateway hypothesis is that the roots of the “Old World” suboscines (Eurylaimides) are in the New World. Four well-supported lineages are known, but their interrelationships are uncertain (79, 80). One of these lineages is Sapayoa aenigma of the rainforests of eastern Panama and northeastern Colombia. The other three lineages are tropical African–Southeast Asian lineages, with a few young species reaching Australasia. We estimate the crown radiation of Eurylaimides to be ~37 Ma; thus, biogeography and age suggest that one lineage or possibly two lineages independently colonized the Old World, with Sapayoa being relictual. If our estimate for the age of crown Eurylaimides at ~37 Ma is correct, then it implies that these lineages entered the paleotropics via Beringia, not across the North Atlantic.

A key event in avian evolution was the diversification of songbirds (Passeri). Our reconstructions indicate that dispersion into East Gondwana of the Acanthisittis probably occurred independently of Passeri (25, 81) (Fig. 3), and we place the most recent common ancestor of the latter on the Australian landmass at 47.3 Ma (HPD, 43.1 to 51.6), which is younger than current estimates (24, 82, 83). Over the next 5 to 7 Ma, oscines underwent substantial phenotypic and ecological evolution in greater Australia; by ~40 Ma, this had resulted in the endemic corvidian radiation and early lineages that reached Zealandia (Fig. 3). Contemporaneously, oscine lineages were transferred from Australia to Southeast Asia and Africa, including the Eupetidae (40.6 Ma) and the Promeropidae (39.5 Ma), the sister group of the Laurasian Passeridae (Fig. 3). These lineages mark the beginnings of the great passeridan radiation across the paleotropics, Eurasia, and eventually the New World (25). This early Australian-Asian exchange also involved lineages of corvids, including at least stem-vireonids (34.6 Ma), campephagids (34.4 Ma), and pachycephalids (31.7 Ma). These ages are coincident in time with the early northward drift of Australia and are estimates of the origin of stem lineages, not of crown clades, which are younger (for example, the crown age for Eupetidae is 26.8 Ma). By the early Oligocene (around 33.9 Ma), portions of northwestern continental Australia were adjacent to Asia, and collision followed in the Miocene (84, 85). In addition, the Miocene-Pliocene left-lateral motion along the Sorong Fault transported continental slivers to the west toward Asia. Thus, hypotheses of long-distance dispersal across wide ocean gaps (83, 86) may not be necessary to explain this complex avifaunal interchange. Once in tropical Asia by the late Eocene, each of the major songbird lineages radiated extensively into the Oligocene and early Miocene environments of the Afrotopics and Eurasia (Fig. 3) (25, 83, 86). Many lineages then entered North America at various times across an emergent Bering land bridge (25).

Temporal dynamics of avian diversification
To explore the effects of Earth history on avian diversification dynamics, we analyzed changes in diversification rates through time. We found that net diversification rates (speciation − extinction) track changes in global climate over the entire timespan of modern bird evolution: rates increase during periods of climate cooling and decrease during periods of climate warming (Fig. 4A). Relative extinction (extinction/speciation) was low, and periods of increased extinction coincide with periods of high net diversification (Fig. 4B), suggesting that the overall dynamics is dominated by changes in rates of speciation. Environment-dependent birth-death likelihood models, in which diversification rates are functions of a time-dependent environmental variable (87), also indicate that rates of speciation and extinction are negatively correlated with global temperature (table S3).

We propose that this macroevolutionary dynamics is largely the result of climate change inducing biome fragmentation and vicariance (that is, climate-induced vicariance). During major cooling trends of the Late Cretaceous (88) and the Cenozoic (89), tropical biomes would have experienced successive waves of retraction and fragmentation (49, 66, 67), which resulted in population fragmentation and increased risk of extinction across entire faunas, but also increased chances of
speciation among the newly isolated populations (90). Thus, provided that speciation rates were higher than extinction rates, this scenario results in higher net diversification of entire avifaunas during periods of climate deterioration. Conversely, expansion of thermophilic forests during warm periods (49, 66, 67) promoted connectivity and homogenization of avifaunas (also suggested by a wave of worldwide dispersion; Fig. 3), a phenomenon also documented among austral fossil floras (91) and boreal mammalian faunas (68, 75). The final burst of diversification in our analysis occurred soon after the middle Miocene cooling episode, which is associated with global retraction of tropical and mesic biomes and expansion of steppes and deserts (92–95). Therefore, the middle Miocene cooling may have fragmented distributions and increased diversification of not only humid tropical but also subtropical and mesic taxa.

Although climate-induced vicariance predicts a final major burst of diversification during Pleistocene glaciations, this burst cannot be detected in our time tree because of sampling (that is, there are no branching events in the last 10 Ma). That most avian time trees show slowdowns in diversification toward the present (95) seems to falsify this prediction, but apparent slowdowns are likely to be artifacts of nucleotide model misspecification (96), deep gene-tree coalescence (97), and incomplete species sampling (98). Alternatively, climate-induced vicariance can also be compatible with low diversification during the Pleistocene if extinction rates increased more than speciation rates, thus dampening net diversification. Complete and calibrated species trees are needed to resolve this matter.

Other events in Earth history may also have influenced diversification rates in Neornithes. In particular, the rate increase at the end of the Cretaceous occurred near the K-Pg transition, suggesting a possible association with the K-Pg extinction event. Although the rate increase started before the K-Pg transition, coinciding with the latest Cretaceous cooling trend, the magnitude of the rate increase suggests a role for the K-Pg event in increasing rates further. The extent of this effect and its particular mechanisms requires further investigation. Although the K-Pg event marked the extinction of close relatives such as Enantiornithes and basal Ornithurae, the extent to which it affected modern birds directly is unclear from the fossil record because of the scarcity of Neornithes remains before and after the event (6, 17, 29, 96). Our biogeographic reconstructions suggest that Neornithes occupied West Gondwanan continents during the K-Pg transition and, therefore, like other animals and plants (91, 97, 98), may have escaped the catastrophic effects of the impact. On the other hand, if multiple early lineages of Neornithes faced extinction during the K-Pg event, that may have created a false signal of rate increase in the reconstructed phylogenies, in which case the apparent increase is merely a consequence of missing lineages before the event (99, 100). Finally, the big-bang model posits that surviving lineages of Neornithes would have experienced ecological opportunity that may have stimulated diversification (15, 18). In any case, catastrophic extinction events may not be general drivers of diversification in modern birds because they cannot explain changes in diversification rates over most of the Cenozoic (fig. S4). Thus, there are no major meteorite impacts, volcanism, or mass extinctions in the Miocene, when diversification rates increased dramatically (Fig. 4A and fig. S4). Our data suggest, in contrast, that global changes in climate are correlated with changes in diversification rates throughout the entire history of modern birds. Statistical comparison of diversification models
also favors climate over extinction events as drivers of avian diversification (Supplementary Materials). Ultimately, we cannot reject a potential effect of the K-Pg mass extinction event on modern bird diversification, but further research on this matter should consider the potentially pervasive background effect of climate-induced vicariance on diversification.

Climate-induced vicariance may have a prominent role in controlling macroevolutionary rates (90), but it may be difficult to detect in paleontological data sets. Actually, except for a clear signal of mass extinctions associated with catastrophic events, general drivers of temporal macroevolutionary dynamics in terrestrial tetrapods have been difficult to identify (87, 101–103). Climate-induced vicariance may be obscured in paleontological data sets because it results in speciation in fragmented populations that are difficult to detect in a geographically sparse fossil record (104). Conversely, during benign climates, populations expand and have higher chances of being detected, resulting in a bias in which new species remain undetected until they expand during warm periods. This hinders the detection of climate-induced vicariance and creates a false signal of positive associations between diversification and warming in the fossil record.

Climate-induced vicariance has received considerable attention in microevolutionary studies of diversification. There is now widespread evidence of population differentiation and speciation associated with habitat fragmentation and biogeographic refugia (105–110). Climate-induced vicariance also explains how niche conservatism might stimulate speciation (111). Finally, analyses of geographic variation in diversification rates among extant birds also suggest higher speciation and extinction rates in regions with harsher climates (14, 112, 113). Therefore, climate-induced vicariance may explain avian diversification through space and time, providing a unified framework for understanding large-scale biodiversity dynamics in birds.

CONCLUSIONS

We generated a new time tree for modern birds that revealed striking patterns of their evolutionary history. We found that modern birds originated in the early Late Cretaceous in Western Gondwanan continents but did not diversify much until the K-Pg transition. This, combined with the poor overall quality of the Late Cretaceous avian fossil record (96), explains in part the scarcity of fossils of modern birds in the Cretaceous, thus partially resolving the “clocks versus rocks” controversy. Modern birds expanded from West Gondwana to the rest of the world through two routes. One route was a trans-Antarctic interchange during the Paleogene that resulted in the presence of multiple avian groups in Australia and Zealandia. The other route was a North American Gateway, facilitated by an inter-American land bridge during the Paleocene that allowed expansion and diversification of modern birds into the Holarctic and eventually the Paleotropics. The North American Gateway hypothesis explains the presence of numerous neovarian groups in the Eocene of North America and Europe without the need to postulate northern origins for these groups or to reject the importance of Gondwana in early avian evolution.

The new time tree also reveals a striking pattern in which avian net diversification rates increased during periods of global climatic deterioration. This pattern is consistent with a model of climate-induced vicariance in which biome fragmentation triggers speciation pulses across entire avifaunas. Thus, initial rapid radiation of Palaeognathae, Galloanseres, and especially Neoaves can be explained by the Late Cretaceous cooling trend, with perhaps additional effects of the K-Pg mass extinction. Overall, the new time tree reveals that the historical biogeography and diversification dynamics of modern birds was tightly linked to the paleogeographic and climatic history of planet Earth.

MATERIALS AND METHODS

Estimation of clade age from the fossil record

If fossil occurrences belonging to a clade are uniformly distributed between the present and the time of origin of the clade $t_0$, the likelihood of a hypothesized age $\theta$ given the observed fossil age occurrences $t_1, \ldots, t_n$ is simply $1/\theta^n$ for times older than the oldest fossil $t_n$ (41, 43). This likelihood is proportional to the probability density of $\theta$ in the absence of prior information (43). Instead of using the present as the baseline, the age of the most recent fossil can be used as the baseline, in which case the likelihood becomes $1/(\theta - t_1)^n - 1$ for $\theta > t_n$ (42). Therefore, the likelihood depends on the age of the oldest fossil $t_n$, the number of fossil occurrences $n$, and the timespan encompassing those occurrences ($\theta - t_1$). The higher the number of fossil occurrences $n$ and the narrower the timespan between the youngest fossil and clade age, the higher the concentration of the likelihood near the oldest fossil $t_n$. Then, a probability density function is parameterized in a way that replicates the shape of the likelihood. This probability density function can be implemented as a clade age prior in molecular Bayesian divergence time estimation. We also considered the case in which fossil ages have uncertainty, specifically when the oldest or youngest fossils are assigned to a geological time interval that spans more than 1 Ma. In such cases, we uniformly sampled pseudoreplicated sets of fossil ages from the time interval, estimated likelihood distributions for clade age, and computed an average probability distribution across pseudoreplicates. The methodology is explained with an example in Fig. 1. Functions for generating empirical calibration priors from the fossil record in the R language are available at https://github.com/evolucionario/cladeage.

Phylogenetic time-tree analysis

We conducted a Bayesian time-tree estimation in the program BEAST 2 (44) using two molecular data sets: one that emphasizes genomic coverage and another that emphasizes taxonomic coverage. The genome-scale data set consisted of the first and second codon positions of 1156 clocklike exons for 48 species from Jarvis et al. (3), which we filtered for missing data (positions with missing data or gaps for any taxa were deleted), and resulted in a final alignment of 124,196 bases. To maximize taxonomic coverage, we used sequences of the slowly evolving recombination-activating genes (RAG-1 and RAG-2) for 230 species representing 202 families and all avian orders (alignment length, 4092 bases). Amplification and sequencing protocols for new RAG sequences followed previous studies of avian RAGs (25). For the RAG alignment, we determined an optimal substitution model and partitioning scheme simultaneously using the PartitionFinder algorithm (114). The genomic data set was analyzed under a single GTR+ gamma substitution model. Bayesian inference was performed using BEAST 2 (44). Rate heterogeneity across lineages was modeled with a relaxed lognormal clock (39). Priors on rates of substitution and clocks were set to defaults (as in Beauti 2.1). We ran analyses using a birth-death tree prior with incomplete sampling that takes into account the fact that we sampled a small fraction of all avian diversity (Supplementary Materials). Priors on calibration clades were set using exponential or log-normal functions, with parameters chosen as
to mimic the empirical density distributions for the origin of clades (fig. S1 and table S1). We ran analyses without sequence data to evaluate the behavior of calibration priors (115). The tree topology of the RAG data set was estimated together with divergence times, except for some clades (Fig. 2B) that were constrained to match relationships supported by recent multi locus and genomic analyses (3, 28). The tree of the genomic analysis was fixed to the ExaML Total Evidence Nucleotide Tree topology of Jarvis et al. (3). Posterior samples were obtained from six independent Markov chain Monte Carlo runs of 80 million generations, each of which sampled every 8000 generations for the RAG data set, and from four runs of 60 million generations sampled every 6000 generations for the genomic data set. Adequacy of sampling and convergence was evaluated by examining the traces and effective sample sizes of likelihoods and parameters.

Ancestral area reconstruction
We divided the globe into eight regions that reflect both current global distributional patterns and major continental plates to ensure that area definitions are meaningful throughout the Cenozoic (Supplementary Materials). We assigned regions to the tips of the tree based on the current distribution of the clades they represent (data set 2). Regions were coded as different states of a single character, and clades distributed across multiple regions were treated as “polymorphic.” We reconstructed ancestral areas using Fitch parsimony, a nonparametric method that implies an island model (116). This method assumes geographic transitions rather than agglomeration of ancestral areas and is appropriate when transitions are rare (116, 117)—two conditions that may be more appropriate for large biogeographic regions because most avian species are restricted to single continents among which dispersal events are rare. In addition, more complex methods require complete phylogenies in which the tips of the tree are individual lineages (116, 118). In the present case, because the tips of the tree are solely representatives of clades, some of which are large, statistical methods may result in biased parameter estimates, compromising ancestral area estimation. Parsimony optimizations were obtained using the function ancestralpars in the phangorn library (119) with the option MPR to obtain all possible parsimony reconstructions. Nevertheless, to explore the effect of methodological assumptions, we also used a probabilistic dispersal-vicariance likelihood model implemented in the library BioGeoBEARS in R (118) (Supplementary Materials). We also explored the effect of using an alternative tree topology (4) (Supplementary Materials). The fossil record indicates that many taxa, which are today restricted to tropical latitudes, were once present in the northern continents (29); therefore, including only extant taxa can bias ancestral reconstructions toward tropical areas. To minimize this bias, we added 25 fossil taxa to the tree representing Holarctic distributions for clades now restricted to the tropics (data set 2). Fossil taxa were attached at the midpoint between their age and the stem age of the clade to which they belong, using a new R function (available at https://github.com/evolucionario/fossilgraft), and treated as terminals in biogeographic reconstructions.

Diversification dynamics analysis
To analyze variation in diversification rates through time, we estimated rates for 5-Ma intervals using the results of the RAG data set and the function bd.ME.optim in the TreePar library (120). We analytically accounted for missing taxa using the option “groups” (121) in which we specified the actual number of species in taxa represented by each terminal of the tree; the richness of each terminal taxon was estimated using current taxonomic knowledge (122, 123) and can be found in data set 2. We also fitted environment-dependent birth-death models in which diversification rates are functions of a time-dependent environmental variable (87): we modeled different scenarios in which speciation or extinction rates vary through time as functions of changes in paleotemperatures. Deep-sea paleotemperatures were derived from a global compilation of benthic foraminifera oxygen isotope (δ18O) data (124) and new estimating equations (125). Rate dependence on global temperature could be linear \[ r(t) = r_0 + aT(t) \] or exponential \[ r(t) = r_0 e^{aT(t)} \], in which \( r_0 \) and \( a \) are estimated parameters and \( T(t) \) is a function that describes changes in temperature over time, in this case, a smooth-spline function with 50 degrees of freedom of deep-ocean temperature data.

SUPPLEMENTARY MATERIALS
Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/1/11/e1501005/DC1

REFERENCES AND NOTES
1. J. Cracraft, in The Howard & Moore Complete Checklist of the Birds of the World, Volume 1, E. C. Dickinson, L. Christidis, Eds. (Aves Press, Eastbourne, UK, ed. 4, 2013), pp. 21–43.
2. J. Cracraft, in The Howard & Moore Complete Checklist of the Birds of the World, Volume 2, E. C. Dickinson, L. Christidis, Eds. (Aves Press, Eastbourne, UK, ed. 4, 2014), pp. 17–45.
3. E. D. Jarvis, S. Mirarab, A. J. Aberer, B. Li, F. Houde, C. Li, S. Y. Ho, B. C. Faircloth, B. Nabholz, J. T. Howard, A. Suh, C. C. Weber, R. R. da Fonseca, J. Li, F. Zhang, H. Li, L. Zhou, N. Narula, L. Liu, G. Ganapathy, B. Bossaux, M. S. Bayzid, V. Zavidovych, S. Subramanian, T. Gabaldón, S. Capella-Gutiérrez, J. Huerta-Cepas, B. Rekpealli, K. Munch, M. Schierup, B. Lindow, W. C. Warren, D. Ray, E. E. Green, M. W. Bruford, X. Zhan, A. Dixon, S. Li, N. Li, Y. Huang, E. P. Derryberry, M. F. Bertelsen, F. H. Sheldon, R. T. Brumfield, C. V. Mello, P. V. Lovell, M. Wirthlin, M. P. Schneider, F. Prosdocimi, J. A. Samaniego, A. Vargas Velázquez, A. Alfaro-Núñez, P. F. Campos, B. Petersen, T. Schizrops-Ponten, A. Pas, T. Bailey, P. Scofield, M. Bunce, D. M. Lambert, Q. Zhou, P. Perelman, A. C. Driskell, B. Shiapiro, Z. Xiong, Y. Zeng, S. Liu, Z. Li, B. Liu, K. Wu, J. Xiao, X. Yinxi, Q. Zheng, Y. Zhang, H. Yang, J. Wang, L. Smeds, F. E. Reidnitt, M. Braun, J. Fjeldså, L. Orlando, K. Barker, K. A. Jønsson, W. Johnson, T. C. Glenn, J. McCormack, D. Burt, H. Ellegren, P. Alström, S. V. Edwards, A. Stamatakis, K. P. Koepfl, S. O’Brien, D. Haussler, O. A. Ryder, C. Rahbek, E. Willerslev, G. R. Graves, T. C. Glenn, J. McCormack, D. Burt, H. Ellegren, P. Alström, S. V. Edwards, A. Stamatakis, D. F. Mindell, J. Cracraft, E. L. Braun, T. Warnow, W. Jun, M. T. Gilbert, G. Zhang, Whole-genome analyses resolve early branches in the tree of life of modern birds. Science 346, 1320–1331 (2014).
4. R. O. Prum, J. S. Berv, A. Domburg, D. J. Field, J. P. Townsend, E. M. Lemmon, A. R. Lemmon, A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. Nature 526, 569–573 (2015).
5. P. G. P. Ericson, C. L. Anderson, T. Britton, A. Elzanowski, U. S. Johansson, M. Killenjø, J. I. Ohlson, T. J. Parsons, D. Zucco, G. Mayr, Diversification of Neoaves: Integration of molecular sequence data and fossils. Biol. Lett. 2, 543–547 (2006).
182. K. P. Burnham, D. R. Anderson, Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (Springer, New York, 2002), 488 pp.
183. C. A. L. Bailer-Jones, Bayesian time series analysis of terrestrial impact cratering. Mon. Not. R. Astron. Soc. 416, 1163–1180 (2011).
184. V. E. Courtillot, P. R. Renne, On the ages of flood basalt events. C. R. Geosci. 335, 113–140 (2003).
185. O. Eldholm, M. F. Coffin, in The History and Dynamics of Global Plate Motions (American Geophysical Union, Washington, DC, 2000), pp. 309–326.

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Author contributions: S.C. and J.C. conceived the study. S.C. devised and implemented the clade age prior estimation method and diversification analyses, and compiled the fossil, richness, and biogeographic data sets. S.C. and J.C. designed and conducted the time-tree analyses and biogeographic reconstructions. S.C. and J.C. wrote the manuscript. Competing interests: The authors declare that they have no competing interests. Data and materials availability: All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors. New sequences were deposited in GenBank (KT954347 to KT954541), whereas alignments and maximum clade credibility trees were deposited in TreeBASE (http://treebase.org; submission 17445). Databases of fossils used for calibration (data set 1) and the biogeographic and species richness data (data set 2) are available as online supplementary materials.

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Supplementary Materials for

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This PDF file includes:

Text
Fig. S1. Probability density distributions for the age of the most recent common ancestor (crown age) of 24 avian clades in the RAG data set inferred from the distribution of fossil occurrences.
Fig. S2. Biogeographic ancestral area reconstruction using Fitch parsimony optimization.
Fig. S3. Alternative biogeographic ancestral area reconstructions.
Fig. S4. Diversification through time of modern birds and Earth history events.
Fig. S5. Effect of the tree prior on Bayesian divergence time estimation.
Table S1. Probability distributions of clade age from fossil occurrences, used as calibration priors in Bayesian divergence time analysis in BEAST 2.
Table S2. Reconstructions of the taxonomic composition of Late Cretaceous–Cenozoic global avifaunas.
Table S3. Environmental birth-death models of the associations between diversification rates and global temperature in modern birds.
Table S4. Birth-death shift models representing associations between Earth history events and diversification rates in modern birds.
References (126–186)

Other Supplementary Material for this manuscript includes the following:
(available at advances.sciencemag.org/cgi/content/full/1/11/e1501005/DC1)

Data set 1 (Microsoft Excel format). Fossils used for calibration.
Data set 2 (Microsoft Excel format). Biogeographic and richness information.
Supplementary Text

Selection of calibration clades and fossils

Because the oldest fossil that belongs to a clade plays a critical role in setting the minimum possible age for a clade, we first based the selection of calibration nodes on the existence of a good quality and formally described fossil composed of multiple bones and whose affinities were established by phylogenetic analysis or the presence of unambiguous derived characteristics. To ensure all major avian groups contained at least one calibration node, in a few instances we considered fossils consisting of a single bone if their phylogenetic position was unequivocal (see below and data set 1 for details). Once a candidate clade was identified, we searched the literature for the first fossil occurrence of each clade in each of nine major geographic regions of the world: South America, North America, Europe, Africa, Madagascar, Asia, Australia (including New Guinea), Zealandia, and Antarctica. For oceanic birds, we also ensured that records in different continents were not in close proximity in the same oceanic region and conversely, in some instances we included fossils from the same continent if they came from different oceanic coasts. We started from global and regional compilations of fossil birds (29, 126–129), complemented by searches in the Paleobiology Database (http://fossilworks.org) and Google Scholar (http://scholar.google.com). We evaluated each candidate fossil individually based on the original descriptions and subsequent published analyses. In two instances, the geographic origin of the clade was unquestionable (Casuariiformes, Artamidae); in those cases, we used the oldest record of each fossil species (see data set 1) to generate the age prior.

The likelihood function used to generate a distribution for clade age assumes that fossil finds are distributed uniformly through time (36, 37). We tested for departures from a uniform distribution using a Kolmogorov-Smirnov test in R (function ks.test). The test requires that the minimum and maximum bounds of the distribution are known, so we used point estimates of these bounds using Ref. (38) equations 4 and 6. In cases of significant departure from uniformity, we discarded the clade entirely or excluded late Paleogene and Neogene fossils. The final list of calibration clades and fossils is given in data set 1. Cases in which the published evidence for the phylogenetic position of the oldest fossil is controversial are discussed next.

Palaeognathae. We used two alternative calibrations for Palaeognathae. For the RAG dataset, we used Diogenornis fragilis Alvarenga 1983, considered the oldest record of stem Rheiformes (29, 130), as the oldest fossil of a clade of "higher ratites" (all crown- paleognaths except for Struthioniformes) (12, 131–133). Although Diogenornis has not been included in a phylogenetic analysis, the fossil shows marked similarity to extant Rheidae. For the genome dataset, we used an alternative calibration based on Lithornis. A recent analysis combining molecular and osteological data placed Lithornis as sister to Tinamiformes and thus part of crown Palaeognathae (133).

Crown Casuariiformes. The fossil genus Emuarius from the late Oligocene and early Miocene of Australia sets a minimum possible age for crown Casuariiformes (Casuariidae and Dromaiidae). Emuarius gidju (Patterson & Rich 1987) from Riversleigh sites is now known from multiple bones, including the cranium, the oldest being ca. 24 Ma, and its phylogenetic position as a stem member of the Dromaiidae was confirmed by phylogenetic analysis (134). The slightly older (ca.
25 Ma) *Emuarius guljaruba* Boles 2001 from Lake Palankarinna, known only from a tarsometatarsus, is very similar to *E. gidju* and may turn out to be the same taxon (*134*), therefore, we tentatively treated *E. guljaruba* as the oldest fossil representing crown Casuariiformes. Given the exclusive Australopapuan distribution of all fossil and extant members of this clade, we used the first fossil find of all species from the Australian continent (*data set 2*).

Anatidae/Anseranatidae. *Vegavis iaai* Clarke et al. 2005 from the latest Cretaceous of Antarctica (67 Ma) is the best evidence of a representative of a modern avian order in the Cretaceous (*9*). Although the use of *Vegavis* for calibration as been questioned (*18, 135*), its affinities have been established by phylogenetic analysis (*9*) and its old age is consistent with the long stem branch of Anatidae in uncalibrated molecular trees (*28*). We also used *Vegavis iaai* to set a minimum age for Galloanseres in the genome dataset because nodes within Anseriformes were not sampled in that dataset.

Pelecanoidea. Two contemporaneous fossil birds from the early Oligocene (Rupelian) of Africa and Europe provide a minimum age constraint for the Pelecanoidea, the clade formed by the families Pelecanidae, Scopidae, and Balaenicipitidae. One is *Goliathia andrewsi* Lambrecht, 1930, known from an ulna and a distal tarsometatarsus from quarry M of the Jebel Qatrani Formation, Egypt, assigned to the Balaenicipitidae (*136, 137*) but without an explicit phylogenetic character analysis. New estimates suggest an age between 29.5 and 30.2 Ma for quarry M (*138*). The other fossil is a nearly complete skull and mandible from Luberon, France, that is identical in all details to extant pelicans (*139*). Together, these two fossils set a minimum possible age for the Pelecanoidea.

Pandionidae/Accipitridae. The early Oligocene specimen PW-2004/7-LS is an ungual phalanx identified as an ancient osprey (*140*). Although it is a single bone without a scientific name, ungual phalanges of ospreys are very characteristic and show two derived characters not observed in other birds of prey (*29, 140*). For this reason, even if fragmentary, we consider this fossil to belong to the Pandionidae and it becomes the earliest unambiguous record of the crown clade formed by Pandionidae and Accipitridae.

Tyranni/Passeri (eupasserines). The early Oligocene *Wieslochia weissi* Mayr & Manegold 2006 was described as a passerine most similar to suboscines but whose subordinal affinities could not be determined (*141*). However, like all suboscines of the suborder Tyranni, the ulna of *Wieslochia* has a well-developed tuberculum ligamenti collateralis ventralis (*141*). The corroboration of a sister relationship between Passeriformes and Psittaciformes and the basal position of Acanthisittidae indicate that this morphology is a derived state of the suborder Tyranni; Psittaciformes, Zygodactylidae, Acanthisittidae, and the suborder Passeri do not have a well-developed tuberculum (except for representatives of Hirundinidae and Bombycillidae, *142*). A well-developed processus procoracoideus also suggests Tyranni affinities (*141*). In contrast, characters that suggest a more basal position of *Wieslochia* are ambiguous. For example, although six ossified tendinal canals are a synapomorphy of the hypotarsus of Eupasserines (*143*), the ossification of the hypotarsus is variable in Tyranni and open (only partially ossified) tendinal canals are found in several members of the Furnarioidea (*144*). Therefore, we conclude that *Wieslochia* belongs in the suborder Tyranni and therefore sets a
minimum age for crown Eupasseres, the clade formed by Tyranni and Passeri. In addition, there is an articulated hand (SMF 504) from Luberon, France, of the same age that also shows a derived character of the Tyranni in the distal carpometacarpus (145). Older remains previously attributed to Passeriformes (146) are too fragmentary and may not even belong to this order (135), and other fairly complete specimens from the early Oligocene of Europe cannot be assigned to any of the three passerine suborders (147, 148).

Certhioidea. Certhiops rummeli Manegold 2008, described from a tarsometatarsus from the early Miocene of Germany, shows derived characteristics of members of the superfamily Certhioidea that climb tree trunks (149). Although there is strong support for the Certhioidea, including the non-climbing Troglodytidae and Polioptilidae, relationships within it are not well resolved, and the climbing families Certhiidae and Sittidae may not form a clade (150, 151). In any case, short internodes among Certhioidea families (151, 152) constrain the possible branching of the fossil lineage to a narrow time window. Therefore, we use Certhiops to set a minimum age for crown Certhioidea.

Emberizoidea (nine-primaried oscines). Palaeostruthus hatcheri Shufeldt 1913 was described based on a complete maxillary rostrum from the late Miocene of Kansas, USA. Although no formal phylogenetic analysis has been conducted, details of this complex bone allow assignment to the Passerellidae, and the rostrum is extremely similar to the extant Ammodramus savannarum (153). However, given the polyphyly of Ammodramus (154), implying rapid homoplastic evolution, we consider relationships of Palaeostruthus within the family unresolved. Therefore, Palaeostruthus sets a minimum age for the clade formed by Passerellidae and its sister group. Because relationships among families in the Emberizoidea are not well resolved (155) we used Palaeostruthus and the fossil record of the Emberizoidea to calibrate this radiation, represented by Emberiza and Thraupis in the RAG dataset.

**Optimal partitioning scheme and substitution model**

For the RAG dataset, we determined an optimal substitution model and partitioning scheme simultaneously using the PartitionFinder algorithm (114). The maximally partitioned scheme evaluated consisted of a partition by both gene and codon position (six partitions). A preliminary maximum likelihood tree was generated using the maximally partitioned scheme and GTR + Gamma models of substitution in RAxML (156) and used in PartitionFinder. The scheme that minimized the Bayesian information criterion was nearly maximally partitioned with GTR + Gamma models for most partitions except for the second codon position of RAG2 that was grouped with the first codon position of RAG1, and the model for the third codon position of RAG1 that had equal base proportions (the SYM + Gamma model, Ref. 157).

**Bayesian divergence estimation and evaluation of priors**

We ran the main analyses using a birth-death tree prior with incomplete sampling (158) that takes into account that we sampled a small fraction of all avian species diversity; using the ‘birth-death skyline contemporary’ prior, part of the BEAST BDSKY 1.1.0 add-on (159), we set
a uniform prior (0, infinity) for the birth/total death ratio (effective reproduction number R0), a uniform prior (0, infinity) for the “total death” rate (“become uninfected”) prior, and a prior for the sampling probability (rho) to take into account uncertainty regarding the total number of extant avian species: we set the parameters of a beta distribution so that it resulted in a bell-shaped distribution with the 5% quantile at 0.023, the proportion of the currently assumed 10,000 avian species in the RAG dataset (0.0048 for the genome dataset), and the 95% quantile at 0.008 (0.0016 for the genome dataset), corresponding to assuming about 30,000 extant avian species.

The sample from the prior showed that all clade-age priors behaved as expected except for the prior on the Tyranni-Passer (Eupasserines) clade, which produced much older ages than the empirical density based on fossils. We suspect that this is an effect of the tree prior inducing an old age for a clade of high diversity like Eupasserines. A more restrictive calibration density—Gamma (1.3, 0.7)—was required to produce a prior similar to the empirical density.

We also repeated the analysis with a simple Yule prior to assess the sensitivity of our results to tree prior specification. The tree prior had a noticeable influence on the results. With the Yule tree prior, which assumes that all extant species are included, younger divergences are underestimated and basal divergences overestimated when compared to the birth-death-sampling prior (Fig. S5). This effect is expected given that deleting terminals from a phylogenetic tree randomly results in relatively longer terminal branches and shorter basal branches. The genomic dataset was more robust to the effect on younger divergences but not on basal divergences (Fig. S5). On the other hand, age estimates around the K-Pg transition are not affected much by the different tree priors. This effect of the tree prior may be a common cause of overestimation of basal ages in divergence time estimation, increasing the gap between fossils and molecular estimates, even when using genomic datasets. Therefore, careful selection and justification of the tree prior and evaluation of its effects should be integral part of any Bayesian divergence time study.

The final analysis used the birth-death-sampling prior. The first 12 million generations were discarded for each of the six MCMC runs, after which all traces showed stationarity. All runs converged and ESS values were above 200 for all parameter except for the age of Eupasseres, which we attribute to the conflict between the tree prior and the calibration density mentioned above. The coefficient of variation of the clock rate was between 0.63 and 0.80 (95% highest posterior density), indicating that a lognormal relaxed clock was an appropriate model of rate heterogeneity across lineages (i.e. the data were not strictly clock-like nor conforming to an exponential relaxed clock).

**Ancestral area reconstruction**

Areas for ancestral reconstruction were a mixture of traditional classifications of zoogeographic regions (160) and major continental landmasses, reflecting a compromise between current patterns of distribution of clades and the history of paleogeographic configuration of the continents. We did not use the Neotropical region as an area; its northern limits lie on the North American and Caribbean plates but many of its component taxa are clearly of South American origin (e.g. Tinamidae, New World suboscine passerines). Conversely, some Central American
and Caribbean taxa considered Neotropical may have originated in the tropical southern realms of the North American continent (e.g. Todidae). For Africa, we considered the Afrotropical region for coding taxa since taxa of northern arid lands (including the Arabic peninsula) have clear Palearctic affinities. The Australian continent (including New Guinea) and Zealandia (including New Caledonia) were treated as two different regions.

To explore the effects of different methodological assumptions and tree topologies, we performed two additional biogeographic reconstructions. First, we used a dispersal-vicariance likelihood model (DIVA-like) implemented in the library BioGeoBEARS in R (118). DIVA-like is a probabilistic model implementation of the parsimony-based DIVA algorithm, (161), in which dispersal, speciation, and extinction are modeled in an explicit way; in particular, DIVA includes a classic vicariance scenario in which speciation results in the split of a widespread ancestral geographic range. No dispersal matrices or time stratification were used. This analysis was performed using the same tree as our main analysis. Second, we reconstructed ancestral areas using Fitch parsimony (116) but using an alternative tree topology. We rearranged the MCC tree of our RAG dataset so it matched the topology of a new proposed tree for Neornithes (4). This new topology has several differences with our MCC, especially at the base of the Neoaves radiation. After rearranging our MCC tree in Mesquite (162), we recovered an ultrametric tree again by using the “mean path length” algorithm (163) implemented in the function chronoMPL in the ape library (164). Finally, we added the fossil taxa as before and reconstructed ancestral areas using function ancestral.pars in the phangorn library (119) with the option MPR to obtain all possible parsimony reconstructions.

These two alternative methods resulted in ancestral area reconstructions similar to those of the main analysis (compare Fig. S2 and Fig. S3). All analyses identified South America as the ancestral area of Neornithes and its three main subclades Palaeognathae, Galloanseres, and Neoaves. Therefore, this result is robust to changes in model assumptions and tree topology. Because the DIVA-like model favors ancestors distributed across multiple areas before speciation, a signal of dispersion out of South America appears earlier than in the Fitch optimization in which area transitions can occur anytime along the descendant branches. The alternative analyses show greater uncertainty regarding the ancestral area of Passeriformes and Psittaciformes, for which the DIVA-like reconstruction includes Australia and Zealandia, in addition to South America, as possible ancestral areas, suggesting earlier trans-Antarctic connections and the alternative topology resulted in nearly complete ambiguity (Fig. S3). The DIVA-like reconstruction favors Holarctic regions for stem nodes of Psittaciformes, Cariamiformes, and the Steatornithidae-Nyctibiidae clade, which would imply an early participation in the North American Gateway and then recolonization of Gondwanan continents. Alternatively, this may be explained by the influence of the fossil taxa Halcyornithidae, Idiornithidae, Prefica, and Paraprefica, distributed in the northern continents; the fact that they are temporally closer to the ancestral node makes them more influential than extant taxa in probabilistic ancestral-area estimation.

Reconstruction of Late Cretaceous-Cenozoic avifaunas
Traditionally, reconstructions of biotas at a point in space and time have been based largely on direct fossil evidence, which is the gold standard for such inferences. The avian fossil record, while steadily improving, is neither dense nor evenly distributed across the continents but instead is better represented in the Northern Hemisphere (Mayr 2009). Our reconstructions of the taxonomic composition of five global avifaunas (Table S2) are based on a synthesis of data from phylogenetic relationships, the biogeographic and timetree reconstructions of stem-lineages (Fig. 1), and the Paleogene fossil record. We also incorporated knowledge of paleogeography to infer movements of these avifaunas among continents. For example, we inferred presence in North America for taxa of South American origin that reached the Old World (implied by the North American Gateway Hypothesis). The goal is to infer where stem-lineages were distributed in space and time across the avian tree. By integrating diverse lines of evidence it is therefore possible to erect hypotheses about the inclusion of a taxon (stem-lineage) in an avifauna even when there may currently be no direct fossil evidence for its presence (Table S2). This inference instead comes from the other data just noted.

**Taxonomic notes and biogeographic interpretations**

**Palaeognathae.** Few problems in avian history have persisted over time than the interrelationships and biogeography of the palaeognathous birds. Recent analyses using large-scale data sets of both nuclear and mitochondrial DNA, some of which overlaps among studies, have postulated that the flightless ratites are not monophyletic and that tinamous are imbedded inside them, close to moas (12, 131, 132). These studies, and those based on whole mitochondrial genomes (133, 165), have been unable to resolve several key nodes within palaeognaths, although all place the root of the tree between ostriches and the other taxa. All these studies make the assumption that losing flight multiple times is evolutionarily "easier" than is regaining it (in the case of tinamous), therefore different studies postulate multiple long-distance dispersal events across oceans to explain palaeognath distribution on the lands of Gondwana. We think there is still much to learn about palaeognath history, and therefore remain agnostic in this paper about the details of biogeographic scenarios. Our analysis strongly argues for an origin of palaeognaths on Gondwana, and even most of the phylogenetic scenarios of previous authors are largely consistent with vicariance among the southern continents of flightless stem-lineages, even accepting several independent losses of flight. The most perplexing finding is that of the proposed relationships of elephant-birds and kiwis (133), which is based only on whole mitochondrial genomes. We await further evidence based on nuclear loci before speculating on their biogeographic history.

Our parametric biogeographic (Fig. S3) and avifaunal reconstructions, as well as the fossil record, suggest crown palaeognaths were broadly distributed in the Northern Hemisphere certainly by the Paleocene and perhaps much earlier. Multiple fossil taxa are known from the early Paleogene of North America and Europe (Mayr 2009), and the long stem-lineage of palaeognaths suggests they may have been present there sometime in the Cretaceous. The most viable hypothesis at this time is that one or more lineages were transferred from South to North America in Cretaceous-Paleocene times and then to Eurasia, where lithornithids and various Eurasian fossil groups evolved. We also propose that this stem-lineage may have included the
ostriches. The latter have been suggested as being related to Paleogene taxa in the Northern Hemisphere (Mayr 2009), but that hypothesis needs further corroboration.

**Kagu-Sunbittern-Aptornis.** The relationship between the flightless New Caledonian Kagu (*Rhynochetus jubatus*) and the Neotropical Sunbittern (*Eurypyga helias*) has been well supported in multiple studies, and their relationship to other birds (tropicbirds, Phaethontidae) has apparently been solved with whole-genome studies (3). Our analysis is consistent with a late Paleogene vicariance event among South America, Australasia, and Zealandia, although at present these taxa have no fossil record on Australia. We note that the flightless Miocene-Recent New Zealand fossil *Aptornis* is suggested to be related to the Kagu (166, 167), although others have questioned this relationship (168). Placement of *Aptornis* in the Kagu-Sunbittern clade would further suggest a vicariance interpretation for this group.

**Caprimulgiformes.** Relationships among caprimulgiform higher-taxa are still poorly resolved (169). Our time-tree and biogeographic analysis suggest that their diversification began in South America during the Paleocene, with most lineages subsequently participating in the North American Gateway or the trans-Antarctic route (Fig. S2). Contrary to recent suggestions of a Palearctic origin and subsequent colonization of South America (169, 170), we found that stem-hummingbirds are most likely South American in origin (Fig. S2, S3), although some early lineages reached the Palearctic during the Eocene (171, 172).

**Gruiformes, Charadriiformes, Opisthocomidae.** Phylogenomic analysis recovered *Opisthocomus* as the sister-group of Charadriiformes and Gruiformes (3). This entire clade optimizes to South America (West Gondwana) and its origins are estimated to be around the K-Pg transition. The single species of extant Opisthocomidae, the Hoatzin (*Opisthocomus hoatzin*), is tropical northern South American and fossils on that continent are recorded from the Miocene of Colombia (173) and the late Oligocene-early Miocene of Brazil (174). Fossil Opisthocomiformes have been found in the Old World, including the early Miocene of Namibia (174) and Kenya (175) as well as the Eocene of France (176). Motivated by these findings, the argument has been advanced that opisthocomids arose in the Old World and that the current South American distribution is relictual (174, 176). This "out of Africa" hypothesis is taken in isolation without information about higher-level relationships. Relationships among fossil and living taxa are also poorly resolved (176) although the latter authors suggested that the Namibian taxon *Namibiavis* is sister to all others. However, the relationships of opisthocomids to both Gruiformes and Charadriiformes (3) as well as our global biogeographic reconstruction (Fig. 3, Fig. S2) indicate that a South American, not an African, origin is most parsimonious. Probabilistic biogeographic reconstructions are highly ambiguous, including South America, the Palearctic, and Africa, as possible ancestral regions (Fig. S3). Until opisthocomids can be shown to be related to an Old World taxon, the hypothesis that they were part of an early Paleogene North American biota that moved into the tropical-subtropical western Palearctic via a North Atlantic land connection explains more observations than fossil locality alone.

The Gruiformes are now restricted to the Ralloidea and Gruoidea (1, 28). Our optimization recovers a South American (West Gondwana) origin, which follows from basal gruoids being Neotropical (Psophiidae) and that the sister-group of the gruiforms is the Charadriiformes (3), which are also South American in origin. Probabilistic models are more ambiguous, including
Africa as a possible ancestral area (Fig. S3). We recognize that gruiform biogeography is complicated by an incomplete understanding of the phylogenetic placement of Paleogene fossils relative to living gruoids as well as a very poor understanding of relationships among living and fossil Ralloidea. Yet, given the evidence that gruiforms are related to charadriiforms, our biogeographic hypothesis is the most robust to date.

Psittaciformes and Passeriformes. These two sister-taxa optimize as South American/West Gondwanan in origin due to their basal relationships and the fact their immediate outgroups (falconids and the Cariamae) themselves are South American in origin (Fig 2, Fig. S2). Setting our limited sampling of parrots in the context of the larger sampling by previous authors (177–179), our analysis is consistent with a West Gondwanan origin. On our time-tree, parrots show two trans-Antarctic divergences involving South America, one for the Australian radiation and the other for Zealandia. The distributions of outgroups suggest these were two temporally-independent biotic interchanges from South America to East Gondwana, but future evidence may indicate the New World radiation came from East Gondwana, as suggested by the probabilistic reconstructions (Fig. S3). Participation in the North American Gateway is also evident, given the presence of early lineages in the Paleogene of the Northern Hemisphere (29, 180).

A similar argument might be made for the early divergences of Passeriformes, with one event involving the Acanthisiti of New Zealand and a second involving the Passeri. The results of this paper confirm that the use of a geologically calibrated age of ~84-82 Ma for the biogeographic split of Zealandia and West Antarctica for both passerines (23–25, 82) and parrots (177) was inappropriate. Fossils that can be assigned to crown Passeriformes do not appear until the early Oligocene around 32 Ma (135, 181). We found the age of Passeriformes difficult to estimate because of the influence of the tree prior, as mentioned above, and some discrepancy between datasets (genomic dataset: 46.1, 39.8-51.5 Ma; RAG dataset: 53.0, 48.5-58.0 Ma). In any case, our new estimates place the most recent common ancestor of extant Passeriformes in the late Paleocene or early Eocene. The gap between the estimated passerine crown age and its first crown fossils may be partially explained by the scarcity of avian fossiliferous beds in the Paleogene of the southern continents, where passerines began their diversification (23, 24).

Supplementary diversification analyses

We evaluated whether the pattern of diversification through time was influenced by the megadiverse order Passeriformes by pruning Passeriformes out of the tree and repeating the estimates. The analysis without Passeriformes showed trends in net diversification rates similar to those of the analysis with all Neornithes (Fig. S4D). Noticeable differences include higher rates around the K-Pg boundary and during the late Oligocene-early Miocene warm period. The latter effect resulted in a nearly monotonic increase in rates from the middle Eocene to the present.

To evaluate the relative role of climate change, mass extinctions, and post-extinction bursts (big-bangs) as drivers of diversification patterns, we used birth-death-shift models (120). Mass extinction models included constant background speciation and extinction rates punctuated by
instantaneous mass extinctions (modeled as sampling events with function bd.ME.optim.rho) at the K-Pg and Eocene-Oligocene transitions. The other two models included shifts in diversification rates at specified times (function bd.ME.optim): in big-bang models, rates were different 10 Ma after mass extinction events, and in ‘climate shifts’ models, rate shifts coincide with major changes in global temperature. An overall sampling proportion of 0.0228 was used since bd.ME.optim.rho cannot use information on richness for each terminal. No rate-shift was modeled within the last 10 Ma since there were no branching events sampled in the time-tree. We compared models using an information-theoretic approach based on the Akaike Information Criterion and related metrics (18). The statistical comparison of alternative factors affecting avian diversification dynamics using birth-death-shift models strongly favored a model in which shifts in diversification rates coincided with major changes in global temperature (model probability = 1, Table S4).
Supplemental Figures

Fig. S1. Probability density distributions for the age of the most recent common ancestor (crown age) of 24 avian clades in the RAG data set inferred from the distribution of fossil occurrences. Gray vertical lines indicate the age of the oldest fossil, including uncertainty. Red lines show the empirical probability distribution of clade age obtained using the approach outlined in Fig. 1. When the age uncertainty of the youngest or oldest fossil was greater than 1 Ma, the empirical distribution is the average of 500 pseudoreplicates based on ages uniformly sampled from a time interval representing the uncertainty. Black lines are exponential or lognormal probability density functions that mimic the empirical distributions and were implemented as calibration priors in divergence time estimation (Table S1).
Fig S2. Biogeographic ancestral area reconstruction using Fitch parsimony optimization. Ancestral area reconstructions using the Fitch algorithm are shown on the Maximum Clade Credibility tree from the Bayesian divergence time estimation of 230 species of Neornithes with the addition a posteriori of 25 fossil taxa that represent Holarctic distributions for clades currently restricted to the tropics. All possible most parsimonious reconstructions are shown for each node. Distributions at the tips are those of the clades they represent.
Fig S3. Alternative biogeographic ancestral area reconstructions. (A) Ancestral area reconstructions using a dispersal-vicariance likelihood model. Pie charts on nodes show the marginal probability of each geographic region. The tree is the Maximum Clade Credibility (MCC) tree from the Bayesian divergence time analysis of the RAG dataset with the addition a posteriori of 25 fossil taxa that represent Holarctic distributions for clades currently restricted to the tropics. (B) Ancestral area reconstructions using Fitch parsimony on an alternative tree topology (4) (see Supplementary Text for details).
Fig S4. Diversification through time of modern birds and Earth history events. (A) Meteorite impact crater data from (183) including only those larger than 10 km in diameter and standard deviations of age estimates lower than 5 Ma. (B) Large igneous provinces: time range of major activity and original volume from (184), to which we added the Sierra Leone and Maud Rise Provinces from (185). (C) Deep-ocean paleotemperatures estimated from a global compilation of benthic foraminifera oxygen isotope data (124) and equations 3.5 and 3.6 in (125), represented by a local regression smoother and associated 95% confidence intervals. Vertical dashed lines indicate the subdivision of time intervals with different climates used for the “environmental shifts model” model. (D) Net lineage diversification rate (speciation - extinction) estimated for 5 Ma intervals for all Neornithes (red line), excluding the order Passeriformes (gray line and interquartile ranges), and the ‘environmental birth-death-shift model’, in which intervals represent periods with different climates; lines are medians of 500 estimates from a sample of the posterior distribution of trees.
Fig. S5. Effect of the tree prior on Bayesian divergence time estimation. Maximum clade credibility (MCC) trees from a Bayesian divergence time estimation assuming a “birth-death-sampling” prior that incorporates the fact that the only a fraction of extant avian diversity was included: (A) time-tree obtained using ~124 kilobases from the first and second codon position of 1156 clock-like genes of 48 species (genomic dataset); (B) time-tree obtained using ~4 kilobases of the recombination-activating genes (RAG) of 230 species. Red arrows indicate the displacement of nodes in relation to the MCC tree obtained using a simple Yule prior that assumes complete species sampling (tree comparison used function compare.phylo in the phyloch library in R, available at http://www.christophheibl.de/Rpackages.html).
Table S1. Probability distributions of clade age from fossil occurrences used as calibration priors in Bayesian divergence time analysis in BEAST.

| Crown clade                  | Oldest fossil                  | dataset | n  | distribution   | μ    | σ    | offset |
|------------------------------|--------------------------------|---------|----|----------------|------|------|--------|
| Palaeognathae                | Lithornis celetius             | genomic | 8  | log-normal     | 2.1  | 0.9  | 61.7   |
| higher ratites               | Diogenornis fragilis           | RAG     | 4  | log-normal     | 2.8  | 1.3  | 55.8   |
| Casuariiformes              | Emuarius guljaruba             | RAG     | 6  | log-normal     | 1.4  | 1.0  | 24.0   |
| Galloanseres*               | Vegavis iai                    | genomic | 7  | log-normal     | 1.9  | 1.1  | 66.0   |
| Anseranatidae/Anatidae*     | Vegavis iai                    | RAG     | 5  | log-normal     | 1.5  | 1.0  | 66.0   |
| Anserinae/Anatinae          | Mionetta blanchardi            | RAG     | 8  | log-normal     | 1.5  | 0.8  | 23.0   |
| Odontophoridae/Phasianidae  | Palaeorctyx gallica            | RAG     | 4  | log-normal     | 2.5  | 0.7  | 23.0   |
| Phoenicopteriformes         | Adelalopus hoogbutseliensis    | both    | 7  | log-normal     | 1.6  | 0.7  | 30.0   |
| Columbidae                  | Primophaps schoddei            | RAG     | 7  | log-normal     | 1.2  | 1.0  | 24.0   |
| Caprimulgiformes            | Eocypselus vincenti            | both    | 7  | exponential    | 9.0  |      | 54.0   |
| Cursorimorphidae            | Scandiavis mikkelseni          | both    | 7  | exponential    | 9.0  |      | 54.0   |
| Gruiformes                  | Mesaelornis nearctica          | RAG     | 7  | exponential    | 8.5  |      | 52.0   |
| Chionoidea                  | Wilaru tedfordi                | RAG     | 4  | log-normal     | 1.9  | 1.1  | 24.0   |
| Phaethontimorphae           | Lithoptila abounnensis         | both    | 3  | log-normal     | 1.4  | 0.7  | 55.8   |
| Procellarimorphidae         | Waimana manneringi             | both    | 5  | exponential    | 11.0 |      | 61.0   |
| Sulidae                     | Limnophregata azygosternon     | RAG     | 7  | exponential    | 7.0  |      | 52.0   |
| Pelecanidae/Balaenicipitida | Goliathia andrewsi             | RAG     | 5  | log-normal     | 1.8  | 0.8  | 30.0   |
| Pandionidae/Accipitridae    | PW-2004/7-LS                   | RAG     | 6  | log-normal     | 1.7  | 0.8  | 33.9   |
| Coracimorphidae             | Sandcoleus copiosus            | both    | 5  | exponential    | 14.0 |      | 56.4   |
| Picumninae/Picininae        | Picauloides saxicemens         | RAG     | 5  | exponential    | 5.5  |      | 22.5   |
| Polyborinae/Falconinae      | Pedohierax ramenta             | RAG     | 5  | log-normal     | 1.7  | 0.8  | 16.0   |
| Psittacopasserae*           | Palchrapollia gracilis         | both    | 3  | log-normal     | 1.0  | 1.5  | 55.4   |
| eupasseres                  | Wieslochia weissi              | both    | 7  | log-normal     | 1.7  | 0.8  | 30.0   |
| Artamidae                   | Kurrartapu johnngayeni         | RAG     | 2  | log-normal     | 2.0  | 0.7  | 16.0   |
| Certhioidea                 | Certhiops rummelii             | RAG     | 3  | log-normal     | 2.0  | 1.2  | 18.0   |
| Emberizoida                 | Palaeostruthus batcheri        | RAG     | 4  | log-normal     | 1.0  | 1.0  | 9.0    |

Probability distributions are inferred using the method described in Fig. 1. n is the number of fossil occurrence used, μ and σ are the parameters of the probability distributions. The offset for the prior distribution is the upper stratigraphic bound (minimum age) of its oldest fossil. For clades marked with *, late Paleogene and Neogene fossils were excluded to improve uniformity of fossil occurrences. See data set 1 for details of the fossils used.
Table S2. Reconstructions of the taxonomic composition of Late Cretaceous–Cenozoic global avifaunas.

**Late Cretaceous-early Paleogene West Gondwanan Avifauna**

**Confirmed by fossil record:** Rheiformes, Galloanserae (including extinct Pelargornithidae), Phoenicopterimorphae, Cariamiformes, Sphenisciformes, Gaviiformes, Charadriiformes, and Falconidae

**Inferred from ancestral-area reconstructions and/or paleobiogeographic connectivity:** Palaeognathae, Rheiformes, Tinamiformes, Galloanserae, Anhimidae, Cracidae, Neoaves, Opisthocomiformes, Phoenicopterimorphae (Phoenicopteridae + Podicipedidae), Caprimulgiformes, Steatornithidae, Nyctibiidae, Apodi, Gruiformes, Charadriiformes, Phaethontimorphae, Eurypygiformes, Aequornithia, Sphenisciformes, Gaviiformes, Coraciornithia, Cariamiformes, Falconiformes, Psittaciformes, and Passeriformes.

**Paleogene East Gondwanan avifauna**

**Confirmed by fossil record:** Galloanserae, Anseriformes, Coraciornithia?, Sphenisciformes, Charadriiformes?, Passeriformes.

**Inferred from ancestral-area reconstructions and/or paleobiogeographic connectivity:** Dinornithiformes, Casuariiformes, Apterygiformes, Galloanserae, Anseranatidae, Megapodiidae, Podargidae, Charadriiformes, Rhynochetidae, Sphenisciformes, Hemiprocnidae, Aegothelidae, Strigopidae, Cacatuidae, Acanthisitti, Passeri.

**Early to middle Paleogene Holarctic avifauna**

**Confirmed by fossil record:** Palaeognathae, Struthioniformes, Lithornithidae, Galliformes, Phasianoidea, Anseriformes, Mesitornithidae, Phoenicopteriformes, Otidimorphae including Cuculidae + Musophagidae + Otidae, Caprimulgiformes, Steatornithidae, Podargidae, Caprimulgidae, Nyctibiidae, Apodi, Phaethontiformes, Opisthocomiformes, Grui (Messelornithidae?), Charadriiformes, Gaviidae, Pelecaniformes, Coracornithia, Coraciiformes, Leptosomidae, Coliidae, Trogonidae, Coraciidae, Galbulae, Accipitriformes, Strigiformes, Cariamiformes, Psittacidae, Eurylaimides.

**Inferred from ancestral-area reconstructions and/or paleobiogeographic connectivity:** Palaeognathae, Struthioniformes, Lithornithidae, Galliformes, Phasianoidea, Anseriformes, Mesitornithidae, Phoenicopteriformes, Otidimorphae including Cuculidae + Musophagidae + Otidae, Podargidae, Caprimulgidae, Nyctibiidae, Apodi, Phaethontiformes, Opisthocomiformes, Grui (Messelornithidae?), Charadriiformes, Gaviidae, Pelecaniformes, Coracornithia, Coraciiformes, Leptosomidae, Coliidae, Trogonidae, Coraciidae, Galbulae, Strigiformes, Accipitriformes, Strigiformes, Cariamiformes, Psittacidae, Eurylaimides.

**Paleogene African avifauna:**

**Confirmed by fossil record:** Galloanserae (Pelargornithidae), Opisthocomidae, Phaethontiformes.

**Inferred from ancestral-area reconstructions and/or paleobiogeographic connectivity:** Palaeognathae, Galloanserae (including extinct Pelargornithidae), Opisthocomidae, Columbimorphae, Otidimorphae, Coracornithia, Buceroti + Coraciiformes, Balaenicipitidae.

**Paleogene Malagasy avifauna:**

**Confirmed by fossil record:** None
Inferred from ancestral-area reconstructions and/or paleobiogeographic connectivity:
Leptosomiformes, Mesitornithiformes, Couinae, Brachypteraciidae, Philepittidae, and Vangidae.

Avifaunas reconstructed from stem-lineages of extant clades based on the Neornithes time-tree and ancestral-area reconstruction (Fig. 3, fig. S2), paleogeographic models, and the avian fossil record. Paleobiogeographic connectivity was used for some clades lacking fossils in an area and without ancestral reconstructions in the region but their presence is implied by the biogeographic hypothesis (e.g., suboscines in the Paleogene of North America).

Table S3. Environmental birth-death models of the associations between diversification rates and global temperature in modern birds

| Speciation  | Extinction  | K  | L-Lik    | AIC     | ΔAIC | P   |
|-------------|-------------|----|----------|---------|------|-----|
| linear      | linear      | 4  | -927.3   | 1862.6  | 0.0  | 1.00|
| linear      | constant    | 3  | -939.6   | 1885.1  | 22.5 | 0.00|
| exponential | constant    | 3  | -940.1   | 1886.2  | 23.6 | 0.00|
| exponential | exponential| 4  | -940.1   | 1888.2  | 25.6 | 0.00|
| constant    | exponential| 3  | -943.2   | 1892.5  | 29.9 | 0.00|
| constant    | linear      | 3  | -943.2   | 1892.5  | 29.9 | 0.00|
| constant    | constant    | 2  | -943.2   | 1890.4  | 27.8 | 0.00|

Number of parameters (K), log-likelihood (L-Lik), Akaike information criterion (AIC), AIC difference (ΔAIC), and model probability (P).

Table S4. Birth-death shift models representing associations between Earth history events and diversification rates in modern birds

| Description                      | K  | L-Lik    | AIC     | ΔAIC | P   |
|----------------------------------|----|----------|---------|------|-----|
| Shifts with temperature changes  | 14 | -909.6   | 1847.2  | 0.0  | 1.00|
| Different rates during 10 Ma after E-Og | 6  | -931.5   | 1875.0  | 27.8 | 0.00|
| Different rates during 10 Ma after K-Pg and E-Og | 10 | -927.9   | 1875.8  | 28.6 | 0.00|
| E-Og mass extinction             | 3  | -941.5   | 1889.0  | 41.8 | 0.00|
| Uniform birth-death model         | 2  | -943.2   | 1890.4  | 43.2 | 0.00|
| K-Pg and E-Og mass extinctions    | 4  | -941.6   | 1891.2  | 44.0 | 0.00|
| K-Pg mass extinction              | 3  | -943.2   | 1892.5  | 45.3 | 0.00|
| Different rate during 10 Ma after K-Pg | 6  | -942.7   | 1897.4  | 50.1 | 0.00|

Number of parameters (K), log-likelihood (L-Lik), Akaike information criterion (AIC), AIC difference (ΔAIC), and model probability (P).