



'Big bang' for tertiary birds?

Alan Feduccia

Department of Biology University of North Carolina Chapel Hill, NC 27599-3280, USA

The early evolution of living birds has been sharply debated, with two disparate interpretations. Molecular-clock studies consistently date the emergence of modern bird orders at ~100 million years ago or older, coincidental with major continental breakup. This is supported by some biogeographers who use phylogenetics, accept an ancient evolutionary origin and use historical geology to guide their reasoning. The fossil record, however, provides evidence that modern birds represent an explosive Tertiary radiation, following the Cretaceous–Tertiary cataclysm, and their origins are almost 50 million years younger than that predicted by molecular studies. Here, I argue that this explosive, punctuated model conforms to the typical pattern of vertebrate evolution characterized by rapid diversification following a major extinction event.

Dinosaurs, pterosaurs, marine reptiles and two-thirds of all marine life became extinct with the termination of the Cretaceous Period. Yet, according to many recent molecular studies, birds, the vertebrates most sensitive to environmental disturbance, passed unscathed through the apocalyptic cataclysm that ended the Cretaceous [1], along with modern mammals [2–8].

Whether Cretaceous–Tertiary (K–T) extinctions at 65 million years ago (Mya) were gradual or cataclysmic has been debated, but most current evidence indicates that environmental changes led to a stressed biosphere before the end of the Cretaceous and many taxa were on the decline [9]. Agents of environmental disturbance included widespread volcanism, as evidenced by the massive Indian Deccan flood basalt traps [9,10] (which began about one million years before the impact event), mountain building and regression of continental seaways. Regardless of whether an asteroid strike was the only factor in the K–T extinctions, the possibility must be considered that such an impact was the proverbial 'straw that broke the camel's back' [9].

Yet it is now clear that a monumental impact terminated the Cretaceous, producing a simultaneous global iridium anomaly [1]. The bolide that produced the Chicxulub crater (Yucatan) was some 10 km in diameter and crashed into Earth with a velocity of 90000 km h⁻¹, producing minimally a 100-million megaton blast; there might have been multiple impacts, leaving no southern hemisphere refugia [10,11]. Coinciding with, and preceded by massive global volcanism, debris hurled into the atmosphere would have caused a veritable disaster [12], with blackout of the sun and obvious consequences (e.g. a prolonged drop in temperature). In addition, global

fires and huge tsunamis destroyed forests and coastal habitats [1,11].

Massive extinctions occurred, and the most ecologically sensitive vertebrates, namely birds, would have been the first and most affected victims. It stretches credulity that birds could have sailed through unscathed, as suggested by recent studies [2–8]. I had previously proposed an alternative model [13,14] hypothesizing that 'birds endured massive extinctions, underwent a K–T bottleneck, and closely paralleled mammals in their explosive phyletic evolution in the early Tertiary' (Fig. 1). The timetable for this model found subsequent support from gap analyses and new fossil data [14–16].

Models for modern bird evolution

The disparate models for the evolution of modern birds are best illustrated by comparing the 'extinction–explosive evolution model' [13] to the revised classic model of gradualism proposed by Cracraft [6,8], based on cladistic analyses, historical biogeography and molecular data. He concluded that: (1) the origins of modern birds largely occurred in Gondwana; (2) the history of modern birds was largely influenced by the dispersal of the southern continents; and (3) many neornithine lineages arose before, and passed through, the K–T extinction event.

The latter hypothesis closely follows those applying a molecular-clock interpretation to genetic distances among DNA sequences in higher categories [2–8,17,18]. Using differing methods, these studies reach similar conclusions, that: (1) nearly all modern avian (and mammalian) orders arose deep within the Cretaceous, with divergence dates of 100 million years or older; and (2) the breakup of the continents was a major causal factor in the origin of modern orders [2]. Another correlate is that numerous neornithine lineages were resident on late Cretaceous southern continents [6,7], but have not been discovered because of the paucity of fossil localities (Box 1).

Echoing the theme, Cracraft claims that 'involvement of so many neornithine higher taxa in Gondwana is so profound that it is likely that a Southern Hemisphere history will be implicated for additional groups...' and 'continental dispersion isolated ancestors of clades that later diversified on continental land masses...'. [6]. The methodology uses ages of vicariance events from geological data to infer the minimum ages of lineages. However, the traditional model of gradualism and continental dispersal is in conflict with fossil evidence, which albeit hazy, provides immense support for a Tertiary 'big bang' model for bird evolution.

Avifaunal change at the K–T boundary

The K–T boundary is associated with major extinctions [1,19,20] and no group of dinosaurs (traditional

Corresponding author: Alan Feduccia (feduccia@bio.unc.edu).

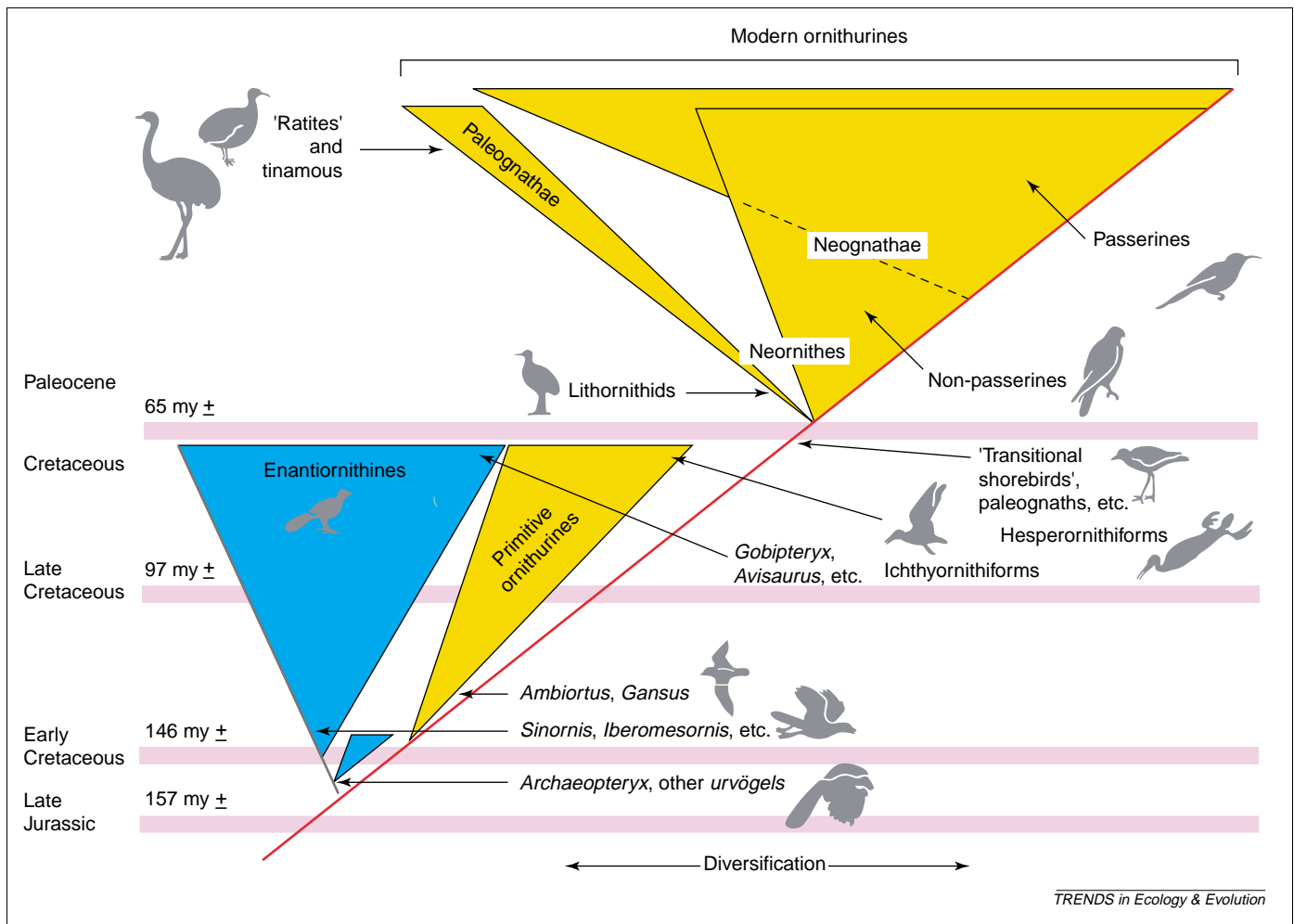


Fig. 1. The Tertiary 'big bang' model for modern bird evolution. A near total demise of archaic birds occurred at the K–T boundary, with a rapid reorganization and explosive early Tertiary evolution from a bottleneck of modern ornithurine morphological types, perhaps involving 'transitional shorebirds' [13,33], paleognaths and some other lineages. The initial diversification of modern ornithurines might have taken place in the late Cretaceous (phylogenetic fuse model), but the explosive adaptive radiation followed the K–T extinction event. This explosive, punctuated model, following a major extinction event, reflects the standard pattern of vertebrate evolution, especially documented following the Permian extinctions. Yellow areas indicate the subclass Ornithurae; blue areas indicate the subclass Sauriurae. Reprinted, with permission, from [13].

meaning), pterosaurs, marine reptiles or ammonites breached the end of the Cretaceous. Many, if not most birds also met their demise. Diverse enantiornithines (known as opposite birds), dominant Mesozoic landbirds, ranging from sparrow- to vulture-sized, occurred in numerous early–late Cretaceous localities, from all continents except Antarctica [21,22] (Box 1). Enantiornithines were abundant during the late Cretaceous, but do not occur beyond the K–T boundary, and are assumed to have become extinct along with the archaic ornithurines [14].

Diverse archaic ornithurine landbirds (non-neornithines) occurred during the early–late Cretaceous along with an assemblage of archaic ornithurine foot-propelled, loon-like divers (hesperornithiforms) [23]. In addition, the tern-like archaic ornithurines (ichthyornithiforms: *Ichthyornis* and *Apatornis*) are known from numerous late Cretaceous localities [14,24]. All archaic ornithurines became extinct at the end of the Cretaceous. Some bony fragments suggestive of modern neornithines are known [23], but no demonstrably modern neornithines, such as shearwaters, petrels, tropicbirds, cormorants, pelicans, gulls, terns, alcids, ducks, and so on, are found in association

with *Ichthyornis* [14]. If these modern ornithurines were present, it would be remarkable that no single bone would be recovered from any of the numerous cosmopolitan late Cretaceous *Ichthyornis* localities. Interestingly, recently described late Cretaceous ornithurines from Mongolia (*Apsaravis*), Argentina (*Limenavis*) [25] and Europe [26] are outside the crown clade of modern neornithine birds, slotting cladistically near *Ichthyornis*. It can therefore be concluded that: 'archaic members of Ornithurae were widespread and successful components of the avifauna during the last stages of the Mesozoic' [25], but absent after the K–T boundary.

The oldest diverse North American avifauna is an early–late Cretaceous (Cenomanian) nearshore marine deposit preserving five taxa (17 individuals) representing two species each of hesperornithiforms, *Ichthyornis* and an enantiornithine [27]. Although again negative evidence, no crown clade ornithurines were recovered.

Large flightless birds are well represented in Tertiary sediments because the bones are heavy and easily preserved. In 1867, Huxley considered the living ratites (ostrich, rhea, emu, etc.) as 'waifs and strays' of an ancient

Box 1. Many fossil localities in southern continents do not yield modern birds

If numerous lineages of neornithines, including passerines [48], were present on the southern continents by the late Cretaceous, it is not apparent from the fossil record (Fig. 1) [49]. Many southern hemisphere Mesozoic bird fossils from diverse localities, including very abundant material from the Campanian of Argentina, are almost exclusively enantiornithine landbirds, along with a few archaic ornithurines and the enigmatic flightless *Patagopteryx*. There are no reliable identifications of any advanced, crown clade ornithurines, and more surprisingly, no ratites. One putative ornithurine is a fossil carpometacarpus that has been provisionally identified as a presbyornithid [50], but such plesiomorphic postcranial elements cannot serve as a signal that the Anseriformes, as we currently diagnose the order, did exist during the Cretaceous.

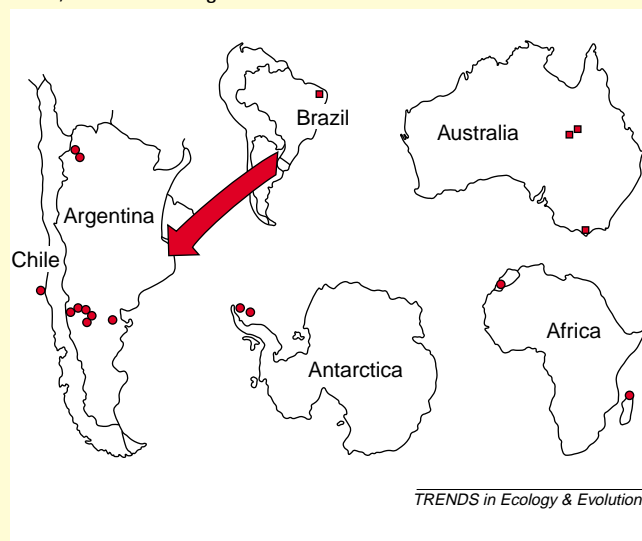


Fig. 1. A map showing 17 diverse Mesozoic fossil bird localities from the southern continents. These deposits yield abundant remains of enantiornithines and other diverse birds, but no confirmed modern ornithurines or passerines. Boxes, early Cretaceous; circles, late Cretaceous. Modified, with permission, from [49].

Mesozoic radiation [14], and Cracraft [6,8] followed this model, viewing ratites as having evolved from flightless ancestors present on Gondwana. Yet, ratites are unknown from Mesozoic sediments and are first known from the mid-Paleocene of Brazil. Lithornithids, volant paleognaths (tinamous-like birds), thought to be ancestral to ratites, were abundant in the northern hemisphere Paleocene–Eocene, and were capable of dispersing to distant land masses (Box 2), including New Zealand and Madagascar [14]. More surprisingly, the oldest known demonstrable ostrich, moa and elephantbird are Lower Miocene, Pliocene, and Plio–Pleistocene, respectively [14,28]. In addition, a giant flightless, late Cretaceous French bird *Gargantuavis* is not a ratite, is not allied with the giant Paleocene–Eocene ornithurines *Diatryma* and *Gastornis*, but is of an archaic ornithurine lineage [29], again indicating no phyletic continuity of ratites or large flightless birds across the K–T boundary.

Fragmentary remains and mosaicism

An additional problem is that the assignment of fragmentary remains of late Cretaceous ornithurines to modern orders lacks credibility [14]. A list of alleged

records of neornithines (modern birds) from the Mesozoic is given in Chiappe and Dyke [30]. As Clarke and Chiappe note [25], ‘the small number of characters preserved in fragmentary material...may often fail to represent the signal from the whole skeleton’. There are numerous misidentifications of late Cretaceous birds, including a parrot [31] and loons [14], and many of the well preserved avian fossils from the Eocene exhibit mosaic skeletons that do not fit neatly into any modern orders as we know them today.

For example: *Rhynchaetites* was described as a shorebird-gruiform, a shorebird, and later found to have an ibis skull. *Juncitarsus* has a tarsus identical to that of stilts, but the skull and humerus are of a flamingo-like bird. *Presbyornis* was described in two different charadriiform families, but its duck-like skull was later discovered. The early landbird *Foro* has individual bones that could be described as cuckoo, touraco (musophagid) or hoatzin, and *Limnofregata* has single bones assignable to booby and frigatebird, as well bones unassignable to any modern group [14,32]. ‘The inadvisability of basing higher taxonomic categories of Paleogene birds [much less Cretaceous birds] on fragmentary limb elements...thus becomes evident.’ [32] Yet, paleontologists continue to make such identifications based on bone fragments from the North American Maastrichtian Lance and Hornerstown Formations (which might be Paleocene) [33,34].

Another observation is that many early Tertiary fossils are basal to lineages. The Lower Eocene London Clay (LC, 53 Mya) tropicbird *Prophaethon* is basal to the pelecaniform assemblage; the LC loon is the primitive gaviiform (loon) *Colymboides*; and the LC galliform is the basal *Paraortygoides* [35,36]. The LC and mid-Eocene Messel parrot *Psittacopes* is primitive and lacks a parrot-like skull [37]. Also present are primitive swifts, coraciiform, piciform and anseriform birds.

A short time period for modern bird evolution

Finally, excluding passerines, most living orders of birds are present in the Lower Eocene LC, only some 12 million years following the K–T extinction event. There are a few bones of a very putative passerine from the Australian Eocene [38]. If a major K–T avian extinction event occurred, the time line for the origin of most bird orders is in the range of no more than 10 million years.

Blind acceptance of the fossil record can lead to erroneous conclusions, but ignoring it can be more serious. The fossil evidence indirectly but overwhelming supports the hypothesis that birds suffered a late Cretaceous demise, with a probable bottleneck of a few morphological forms (possibly paleognaths and ‘transitional shorebirds’ [14,33]) that produced a reorganization, diversification and explosive Tertiary radiation, possibly within a time frame as short as 5–10 million years, paralleling mammals. If all major avian lineages were branching off their phyletic nodes within such a restricted time period, the difficulty of ascertaining phylogenies by cladistic or molecular methodologies is grossly compounded, and many answers might be lost to the past.

Chiappe and Dyke [30] are correct in noting that there is no direct evidence for a sudden disappearance of birds in a

Box 2. The migratory ability of birds renders suspect any speculation on avian origins and biogeography deduced from modern distribution patterns

The difficulty of deciphering avian biogeography is confounded by vast bird migratory abilities, so that reliance on modern distributions is rendered equivocal. A further complication is that the separation of Africa and South America during the late Cretaceous–early Paleocene resulted in a distance that was not vastly greater than that from Ecuador to the Galapagos Islands (much less from Hawaii to mainland areas) [51]. Every tropical or pantropical distribution pattern can be explained as relict, as is the case for parrots, todies, motmots, trogons, bee-eaters, rollers, ground-rollers, and so on [14,52–54]. For example, todies (Todiidae), a family with feeble flight ability, were thought to be a classic example of a group of birds that had evolved *in situ* in the West Indies, until fossils were discovered in the Oligocene of the northern hemisphere [14]. Many taxa that were thought to represent Gondwanan elements (trogons, parrots, etc.) have been discovered as fossils in the Paleogene of Europe or North America [54] and thus represent ‘pseudo-Gondwana’ relict distributions. Deciphering zoogeographical patterns from the current world is particularly difficult because the severity of Pleistocene climatic deterioration left a world in which tropical and subtropical regions became greatly restricted southerly, leaving relict distributions in either old and new world tropics, or pantropical patterns.

Avian flight and migratory ability (Fig. 1) renders impracticable biogeographical analyses from modern distribution patterns. The cattle egret *Bubulcus ibis* vividly illustrates the problem. It invaded South America from Africa in the late 1800s and has subsequently become widespread across North America. Numerous suboscines, thought to have evolved in Gondwana, migrate often several thousand miles, from Alaska and northern North America, to Central and South America. An old world suboscine, the African pitta *Pitta angolensis* can migrate up to 1900 km on an intra-Ethiopian route, and the shining bronze-cuckoo *Chrysococcyx lucidus* travels from New Zealand northward over some

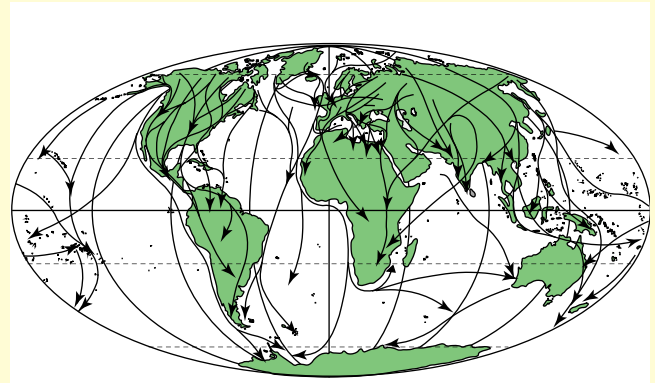


Fig. 1. Important flyways of migrants across oceans and continents. Lines indicate migration patterns for autumn in the northern hemisphere and spring in the southern hemisphere. Modified from [57] and other sources.

3200 km of trackless ocean to the Solomon Islands [14]. Rails, among the poorest fliers, have become distributed across the South Pacific islands, and rapidly evolved flightlessness, in some cases in < 125 000 years [55].

Diamond [56] emphasized the ‘fear of flying’ as perhaps a greater barrier to bird distribution than is geography, but such an assessment is *a posteriori*, deduced from current distribution patterns, and much biogeographical speculation has been subsequently negated by fossil finds.

terminal Cretaceous mass extinction, but the same could be said of the dinosaurs. The ichthyornithiforms have their last appearance ~10 million years before the K–T boundary (J.A. Clarke, PhD thesis Yale University, 2002), but birds slotting cladistically near *Ichthyornis* are younger [26], dating at 65.8 Mya. The record is so sparse that we can only conclude that Mesozoic enantiornithines and archaic ornithurines flourished throughout the Cretaceous and are not recorded past the K–T boundary. Regardless, the cataclysmic event that terminated the Cretaceous must remain a prime ‘suspect’ as an agent of a massive avian extinction.

Fossil record versus molecular analysis

The growing gap between molecular analyses and the fossil record, including the supposed Cambrian ‘explosion’ [39] is astounding. Exemplifying the trend, Kumar and Hedges [2] date the origin of primates at 90 Mya, whereas the fossil record puts the event at 55 Mya [40]. Paton *et al.* [18] rejected a rapid Tertiary evolution hypothesis and a ‘transitional shorebird’ ancestry based on mitochondrial DNA sequences of the highly derived turnstone and oystercatcher, taxa no more hypothetically allied with long extinct ‘transitional shorebirds’ than are any other modern birds. Many of these studies suffer from invalid calibration and inadequate sampling of taxa [41]. Nevertheless, estimated dates for the origins of modern orders are, in millions of years: 100 ± [2], 100 ± [3], 100+ (mammals) [4], 100–120 (Palaeognathae–Neognathae and Galloanserae–Neoaves); 90+ (fowl–ducks); 110 (primate–rodent) [5], and 82–85 (passerines) [7].

If the fossil evidence holds, then one must consider the possibility that there is a serious miscalibration of the molecular clock, if it exists. Commenting on the article by Kumar and Hedges [4], Gingerich noted that if the molecular data are right, the fossil record has a gap of 70 million years. ‘You can imagine how maddening this stuff is to a paleontologist’ [42]. On the other side, Erickson *et al.* note that ‘If the molecular datings are correct, the fossil record of both birds and mammals is severely biased’ [7].

Fossil evidence supports the view that, paralleling birds, mammals represent diverse lineages from either side of the K–T boundary, but no truly modern orders of placentals are known before the Tertiary [43]. Similar to birds, mammals underwent an explosive Tertiary evolution, producing diverse modern orders by the Paleocene–Eocene.

Archaic ornithurines were present in the early Cretaceous of China and elsewhere alongside their enantiornithine counterparts [44], but there is no fossil present that is related to any modern bird order, and no ratite. However, that the radiation of modern birds began deep in the Cretaceous and persisted with minimal disruption through the K–T cataclysm appears untenable, and drifting continents and vicariance biogeography [6,8] have demonstrably little, if anything, to do with the origin and distribution of modern orders of birds. Early diversification might have been rooted in the late Cretaceous [23,30,34] (phylogenetic fuse), but the intense radiation occurred rapidly in the early Tertiary and, although there is little evidence for an exact timescale for bird evolution, the evolution of whales (the ‘poster child’

for macroevolution) from terrestrial ungulates is well documented at <10 million years [45–47].

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