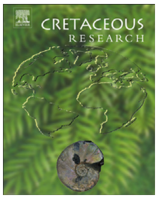
Cretaceous Research 50 (2014) 1–15

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes



Review article

Avian extinction at the end of the Cretaceous: Assessing the magnitude and subsequent explosive radiation

Alan Feduccia

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

ARTICLE INFO

Article history:
Received 22 January 2014
Accepted in revised form 11 March 2014
Available online

Keywords:
Cretaceous
Paleogene
Eocene
K–Pg
Extinction
Aves
Radiation
Cataclysm

ABSTRACT

Debate on the magnitude of Cretaceous extinctions and timing of modern bird origins has sharply coalesced over the past two decades into contested models, gradualistic or explosive. Molecular clocks, bolstered by phylogenetic, biogeographic, and vicariance models, support an Early Cretaceous origin for birds and mammals over 100 million years ago. Yet, although numerous new Chinese fossils of archaic ornithurine birds have been discovered in the Jehol Biota of the Early Cretaceous of China, none shows close affinity to modern neornithines; it is not until the latest Cretaceous when some fossils show more advanced ornithurine morphology, and are possibly Neornithes. In contrast to mass survival scenarios, most paleontological evidence appears to support an explosive radiation following the Cretaceous–Paleogene (K–Pg) mass extinction event, closely paralleling the geometry of mammal evolution. Gradualistic models ignore recent evidence of cataclysmic worldwide events following the impact event. How could mass survival of the environmentally sensitive birds have occurred following cosmopolitan environmental destruction, when other terrestrial vertebrates, particularly ectotherms, suffered dramatic loss? Given the paucity and scrappy nature of avian fossils immediately prior to and after the K–Pg boundary, it is prudent to use mammalian and other biotic evolution in the Paleogene as a guidepost for avian evolution. Our continued inability to produce a veracious phylogeny of higher avian taxa is likely related to a Paleogene explosive burst or 'big bang' evolution of bird and mammal evolution, resulting in short ordinal internodes.

1. Introduction

In 1973, young geologist Walter Alvarez was exploring a limestone gorge outside the medieval village of Gubbio, Italy, when he discovered a curious pencil-thin layer of clay. Shortly thereafter, with Nobel prize winning father Luis Alvarez and two other Berkeley researchers, the team determined that a thin seam contained an unearthly amount of the noble metal iridium, which could only mean a world distribution of ejecta from a huge meteorite impact (Alvarez, 1997). This discovery came only a little over a decade following Eugene (Gene) Shoemaker's monumental 1960 thesis at Princeton "Impact mechanics at Meteor Crater Arizona" and subsequent publication in *Science* (Chao et al., 1960), showing conclusive evidence that Meteor Crater (and by inference Lunar craters) resulted from extraterrestrial impacts, not volcanism. The Shoemaker and Alvarez discoveries added a new dimension to the plate tectonics revolution in revitalizing the field of geology, which had been steeped in uniformitarianism, the view that all Earth history change is gradualistic, including the rate of biological change. Yet, even Darwin's friend Charles Lyell who popularized the concept was baffled by the near total difference between the fossils at the end of the Cretaceous and those at the Paleogene base (Alvarez, 1997:49). Lyell was so welded to this view of Earth history that he postulated an enormous unrecorded geologic time interval the sediment of which had yet to be discovered. We now know that although uniformitarianism "the present is the key to the past" is the underpinning principle of geology, periodic catastrophes have played a major role in Earth history, but it is surprising so much time passed before periodic extraterrestrial causes of extinction would be recognized.

In 1980 the monumental paper by the Alvarez team, "Extraterrestrial cause for the Cretaceous-Tertiary extinction" (Alvarez et al., 1980) appeared in *Science* and the world of geology would never be the same. The Alvarez discoveries rank among the greatest in the history of science; as Walter Alvarez notes, "The is the story of one terrible day in this history of the Earth (Alvarez, 1997:ix)." It was the day some 65.5 million years ago when a giant, 10 km-wide

E-mail address: feduccia@bio.unc.edu.

http://dx.doi.org/10.1016/j.cretres.2014.03.009
0195-6671/© 2014 Elsevier Ltd. All rights reserved.

meteorite slammed into earth at a speed more than 40 times the speed of sound, with an impact equivalent to 100 trillion tons of TNT (10,000 times the world's nuclear arsenal), producing a crater 180 km in diameter in the Yucatán, called Chicxulub, for the nearby the Maya villages (Kring and Durda, 2003). As Walter Alvarez describes it: "A world first dark and frozen, then deadly hot, a world poisoned by acid and soot" (ibid, 1997:14).

2. Armageddon: impact and ejecta

Of more than 2500 papers published following the Alvarez discoveries, every possible speculation on the aftermath of the impact has been aired, but some widely accepted scenarios backed by solid data have emerged. The impact had an array of cataclysmic and complex environmental effects that spread devastation worldwide. Among them was ignition of massive wildfires generated after debris ejected from the crater soared into the atmosphere and rained back to Earth, causing fires to be swept across continents worldwide. The debris was first concentrated above the impact site and at the antipode of impact, on the opposite side of the Earth, at what is now the Indian Ocean (Fig. 1). Estimates suggest some of the material may have reached halfway to the moon before plummeting back to Earth, with reentering debris heating the atmosphere so severely it ignited wildfires from North America to the Indian subcontinent (Kring, 2007; Kring and Durda, 2002, 2003); and rotation of the Earth beneath the returning plume of ejecta resulted in the fires migrating to the west, so that much of the Earth within three days or so was devastated by wildfires. The "ash" (particles of soot) of the Cretaceous world is variously estimated to amount to nearly 70 billion tons of residue. Fires produced severe air pollution, combining with impact-generated dust that choked the sky worldwide, rendered the atmosphere impermeable to sunlight. Thus, photosynthetic plants died and food chains collapsed; it is often likened to a "nuclear winter," with dark, wintry conditions followed by an interval of greenhouse warming. Fires produced debilitating gases such as pyrotoxins, chlorine and bromine, the latter two contributing to the destruction of the ozone layer. Experiments by Kawaragi and colleagues provide evidence that the Earth may have been gassed by a burst of carbon monoxide by impact on carbonates. Shocked carbonates would have released more CO than CO^2, leading to global warming of 2–5 °C for up to several years. They calculate on the basis of simulations of a Chicxulub impact that up to two trillion tons of CO would be released, similar to the mass of CO that could have been generated by firestorms (Kawaragi et al., 2009).

As soot from the fires and dust slowly settled back to ground, sunlight was dramatically, if not totally, attenuated for months, and forests knocked down and burned were first replaced by ferns and algae, as evidenced by a signature "fern spike." The question often posed is just how could anything have survived, but extinctions have biological filters or bottlenecks, and a critical factor may have been uneven distribution of fire, probably including northernmost North America and Europe, and in some regions gymnosperm pollen decreased dramatically but not to zero. In refugia heat was less intense and swamps and their margins provided a somewhat protected environment. Regrowth is estimated to at least 100 years, but may have been 10,000 years (Kring and Durda, 2002, 2003).

The firestorm and subsequent devastating events and pollution generated by the Chicxulub impact combined to produce an environmental disaster ranging from days to months, with reentering ejecta and dust in the stratosphere; it took years for sulfuric acid aerosols to dissipate. Another complication was the near one-million-year-long emplacement of massive volcanism on the Indian subcontinent, the result of which is known as the Deccan flood

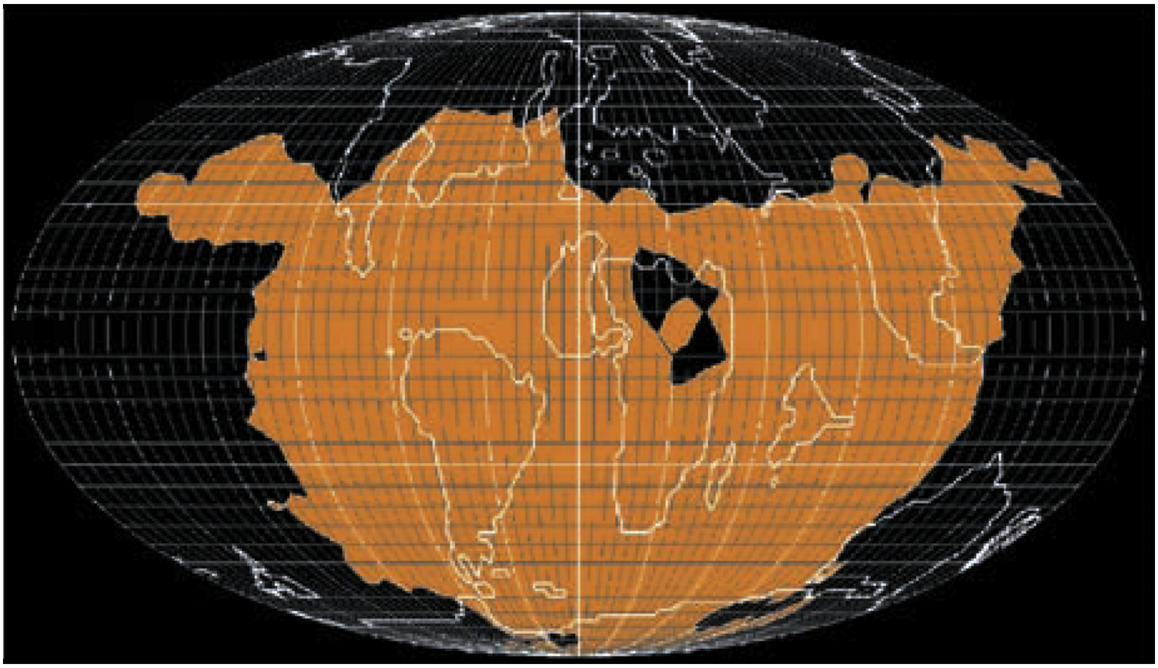


Fig. 1. Global map showing locations where following the Chicxulub asteroid (northwest to southeast impact), the power radiated to the ground was sufficient to ignite vegetation, even if it were initially wet. Clearance of all ejecta may have taken well over a year (from Kring and Durda, 2002). David Kring, Jake Bailey and Daniel Druda have produced an online, computer simulation movie [http://www.lpi.usra.edu/science/kring/epo_web/impact_cratering/enviropages/wildfires.html], showing: "how the fires were ignited, initially around the impact site and, soon afterward, at a spot on the opposite side of the Earth where a concentrated stream of debris rained back down on Earth. As the Earth rotated below the impact ejecta, the fires spread to the west of these two locations over the following hours to days. Fires were ignited in North America, South America, Africa, and Asia. Depending on the trajectory of the impacting asteroid or comet, and details in the expanding plume of impact ejecta, fires may have also been ignited in Antarctica or Europe." (NASA/UA Space Imagery Center's Impact Cratering Series; courtesy, David Kring. Map adapted from: Kring, D. A., and D. D. Druda. 2002. Trajectories and distribution of material ejected from the Chicxulub impact crater: implications for postimpact wildfires. Journal of Geophysical Research, 107(E8):10.1029/2001JE001532), courtesy, Journal of Geophysical Research.

basalts, spanning the K–Pg boundary, which released massive amounts of sulfur and carbon dioxide during voluminous eruptions with devastating effects before and following the impact (Schulte et al., 2010; Keller et al., 2009). Monumental volcanism would have in many respects the same effects as a bolide impact, choking the skies with gases and debris, and blocking the sun, which would have destroyed the food chain. Some geologists have suggested multiple impacts, but more evidence is needed (Chatterjee, 1997; Chatterjee et al., 2006; Mullen, 2004; Keller et al., 2008).

Life was devastated, but biota surviving the bottleneck inhabited a world in which the slate had been wiped clean and vast and diverse ecological zones were available for exploitation (Janzen, 1995). Following the combined cataclysm, evolution in almost all groups of vertebrates was explosive and diverse, even if multiple causes are invoked and extinction in groups like dinosaurs may have been mainly gradual leading up to the impact event (Archibald et al., 2010; Lyson et al., 2011; Brusatte et al., 2012). Most groups were severely affected, with estimates that 75% or more of all species on Earth vanished (Jablonski, 1994). The question posed by this paper is, if such faunal devastation occurred, how is it possible that, as suggested by so many authors using both molecular and paleontological evidence, modern birds first evolved early in the Cretaceous Period, at 100± million years or earlier (Kumar and Hedges, 1998; Brown et al., 2008; Haddrath and Baker, 2012), were distributed in vicariance fashion at the time of continental breakup in the Cretaceous (Cracraft, 1973, 2001a,b), and sailed through the extinction event? (Hedges et al., 1996; Cooper and Penny, 1997; Pacheco et al., 2011). Birds, especially small species and passerines, are on the edge metabolically, a first indicator of environmental perturbation; and non-passerines and the smaller Cretaceous eutherians would have been characterized by lower, but still relatively high metabolic rates. How could these high-metabolic endotherms, with substantial food requirements, not have been affected when many ectothermic groups met their demise?

3. End-Cretaceous extinctions

3.1. Assessing the event

Difficulty in assigning a single cause to end-Cretaceous extinctions rests on a series of events that nearly simultaneously occurred: massive volcanism (among the most massive in Earth history), regression of inland seaways and terrestrial habitat fragmentation, and the extraterrestrial bolide impact (Archibald and Fastovsky, 2004). Some do not cite impact as the primary cause, and tripartite events may have variously caused selective extinctions. Studies of sea-level changes in Texas provide evidence that marine regression profoundly influenced pelagic assemblages, and that the biotic effects of the Chicxulub impact may have been overestimated (Keller et al., 2009). Regardless, we do know that a massive tsunami wave flowed up the land and crossed the Mississippi embayment more than 300 km, with a height of more than 200 m (Matsui et al., 2002); Texas and adjacent areas were particularly hard hit.

Aside from devastating effects on terrestrial vertebrates, two-thirds of all marine animal species disappeared, including extinction of giant marine mosasaurs and plesiosaurs, sharks, mollusks, ammonites, and many species of calcareous plankton, which would collapse the oceanic food chain, but these marine elements will not be discussed here (MacLeod et al., 1997; Koutsoukos, 2005). Many paleontologists believe the K–Pg extinctions to be entirely gradual (Archibald et al., 2010), but many geologists tend to favor the view that there was a sudden mass extinction at the time of impact (Schulte et al., 2010). The latter argue that the correlation between impact-derived ejecta and paleontologically defined extinctions globally bolsters a sudden mass kill off at the boundary between Mesozoic and Cenozoic rocks, at ~65.5 Myr, and that alternative volcanic hypotheses fail to explain the geographic and stratigraphic distribution of ejecta, the timing of mass extinctions, and the scale of environmental changes required for their cause. Yet, regardless of whether some groups were on a gradual decline towards the end of the Cretaceous and the impact was the “straw that broke the camel’s back,” or whether there was a single major cause, the result would have been the same: massive extinctions.

3.2. Plants/fungi/insects

Nichols and Johnson have summarized data for plants using their ability to more precisely date the zones with relation to the K–Pg boundary (Nichols and Johnson, 2008). The first angiosperms appeared in the earliest Cretaceous, followed by rapid diversification during the entire period. Nearly all Cenomanian and post-Cenomanian floras are dominated by angiosperms, and just before the K–Pg event, world floras were conspicuously angiosperm dominated (Cenophytic) in all aspects. The last 5.1 million years of the Cretaceous, the Maastrichtian, is exemplified by floras from North Dakota, characterized by a high percentage of angiosperms with pinnately or palmately lobed leaves, representing up to 30% of species at some localities. Evidence combined from the Upper Cretaceous of North America and eastern Russia show that, a) angiosperms are overwhelmingly dominant and extremely diverse, and b) conifers are vegetatively more common at higher latitudes. So, floral change at the K–Pg boundary occurred in a world where angiosperms were floristically and vegetationally dominant.

Everything temporarily changed in the early Paleocene. Paleocene megafloras are abundant and well-sampled, especially in the western North American Laramide Basins from New Mexico up to Canada, with over 1000 localities, and were quite diverse. However, in the North American lower Paleocene palynofloras are severely reduced in diversity in comparison to those of the Maastrichtian, and a few species dominated numerically. The most striking aspect of lowermost Paleocene floras is the classic “fern-spore spike” at the impact level of stratigraphic resolution. It is apparent that earliest Paleocene plant communities were pioneer communities and in most places these assemblages were dominated almost entirely by a single fern species (Fleming and Nichols, 1990). A modern analog for these pioneer plant fern communities was described by Tschudy (Tschudy and Tschudy, 1986), from the volcanic eruption of Krakatau (Krakatoa) in Indonesia, which wiped clean the vegetation in 1883. Early visitors to the caldera found no plants at all, but a botanist in 1886 found some plants had returned but most were ferns. Another confirmation of the devastating effect of a bolide impact on plant communities came from New Zealand, where Vajda and colleagues documented an equally dramatic fern spike with the large iridium anomaly, indicating again that major climatic perturbations followed an impact winter that was likely preceded by global wildfires (Vajda et al., 2001). Thus, the lower Paleocene palynofloras are characterized more by the absence of Maastrichtian species, than by the presence of new Paleocene taxa, which appear gradually following the fern-spore spike, and grew in a warm greenhouse world, forested from pole to pole.

Corroborative evidence from a fungal proliferation at the K–Pg boundary came from New Zealand where a fungal spike was discovered between the diverse Late Cretaceous palynoflora and the early Paleocene low-diversity fern-dominated section, coincident with the anomaly marking the extinction event. Below this zone the Late Cretaceous coal bears a spore-pollen assemblage containing 80 conifer, fern, and flowering plant taxa typical of complex temperate plant communities (Vajda and McLoughlin, 2004; Vajda et al., 2001). Immediately above this layer the succeeding ~4-mm yielded only fungal spores and fungal hyphae fragments, but followed successively by the low-diversity fern assemblage. The fungal-rich interval is interpreted in this region as wholesale dieback of photosynthetic vegetation at the K–Pg boundary, and the successive fern spike is correlated with similar discoveries in North America.

Maximum extinction estimates vary, but are about 57% for megaflora and 30% for pollen-producing plants from North America sites (Wilf and Johnson, 2004), and in some areas insects and plants suffered substantially at the K–Pg extinction event. In an ingenious study Wilf and colleagues analyzed insect-feeding damage on 14,999 angiosperm leaves from numerous uppermost Cretaceous, Paleocene and lower Eocene sites in western United States. Most Paleocene floras show low plant richness and insect damage, but a low-diversity 64.4-million-year-old Montana flora (just prior to the K–Pg extinction event), shows extremely high insect damage richness, especially of leaf mining species. Yet, an anomalously diverse 63.8-million-year-old flora from the Denver Basin shows little leaf damage and no specialized feeding. These studies thus revealed severely unbalanced insect-plant food webs 1–2 million years following the end Cretaceous extinction, some 65.5 million years ago (Labandeira et al., 2002; Wilf et al., 2006). In addition, there is indirect evidence for extinction in bees, which arose in the mid-Cretaceous along with the co-evolutionary eudicot plants, which are almost entirely dependent on bees for pollination. Extensive molecular phylogenetic analysis on species of Xylocopinae suggest a massive extinction of the group near the K–Pg boundary, with major consequences for subsequent evolution of eudicots and their pollinators (Rehan et al., 2013).

3.3. *Fish*

Fish have traditionally been ignored because many groups are of ancient origin in the Mesozoic (chondrosteans, holosteans) and even earlier (Chondrichthyes), and many survived the K–Pg extinction event, notably sturgeons, paddlefish, gar, Nile bichirs, bowfins as well as sharks and a variety of teleost fishes. The crown of the massive clade of modern fishes, the Acanthomorpha, comprising some 18,000 species, extends deep into the Cretaceous, but is clearly punctuated by the K–Pg mass extinction event, and diversity appears to increase in the wake of the K–Pg boundary, but until recently the impact of the extinction event on acanthomorph evolution remained unexplored. Although teleosts are an ancient group, it now appears that much of the diversification that led to extant groups occurred in the late Mesozoic, but especially the early Cenozoic, a period dubbed the “Second Age of Fishes”(Near et al., 2012).

Friedman reconstructed the trajectory of morphological diversification from its first appearance in the Late Cretaceous to the Miocene using a geometric morphometric database comprising more than 600 extinct species. Data revealed that from the Paleocene to the early Eocene all sampled time units are marked by substantially higher levels of morphological diversity than similar Mesozoic intervals; and percomorphs dominate the acanthomorph fauna throughout Cenozoic time, with dramatic new body forms. Thus, the post-Cretaceous radiation was characterized by proliferation of new anatomical forms and the exploitation of new ecological strategies (Schluter, 2000), and acanthomorphs became dominant in marine ecosystems by the end of the Paleocene, within 10 Myr of the K–P boundary (Bonde, 1997). The major acanthomorph morphological divergence appears confined to the very end of the Cretaceous and early Paleogene (Friedman, 2010).

A persisting question attends the famous cichlids, which have been used as a classic example of a group of primary freshwater fishes (with no salinity tolerance), distributed on Africa and Madagascar, tropical America, the West Indies, and the Middle East and India (and Sri Lanka), presumably as a result drifting Mesozoic continents. An Early Cretaceous origin is typically suggested for the group, based on their seemingly Gondwanan distribution pattern and the timing of the breakup of the Gondwana supercontinent. Another implicit assumption is that ancient cichlids are limited to freshwater and the opening of the Atlantic presented an impassible barrier. But some cichlids today are capable of inhabiting brackish or salt waters (Ward and Wymann, 1977; Whitfield and Blaber, 1979; Oldfield, 2004). If cichlids were present on Gondwana prior to break-up, the minimum age of the family would be at the end of the Early Cretaceous, approximately 120 Myr, and this date appears out of line with the fossil record. The accepted monophyletic Malagasy–South Asian assemblage would require minimally an origin before the end of the Cretaceous, if in fact cichlids of that era were primary freshwater fishes. Largely ignored is the fact that the oldest known fossil cichlids are from a fossil fish assemblage of four or five different families from an Eocene (~46 my) crater lake at Mahenge, Tanzania, including over 400 fish fossils, but cichlids are the major elements.

Recently, Friedman and colleagues assembled a database of known cichlid fossils, comparing it to a catalog of sedimentary rocks formed from freshwater sediments and containing other fishes, from the former Gondwana land mass that could possibly preserve cichlids. They concluded it extremely unlikely that such sediments would not contain cichlids if present during that time, and that the fossil record would have to be on the order of 10–30 times worse in older periods than in more recent times, which is unlikely. They then counted mutations in shared genes of cichlids and close relatives, sequencing 10 nuclear genes from 89 modern cichlids and 69 other fish to arrive at dates when cichlids diverged from their relatives. Their conclusion from fossils and molecules was that cichlids originated long after the Gondwana split, some 65–57 million years ago (Friedman et al., 2013).

3.4. *Squamates*

Although major extinction events have been proposed for vertebrates such as birds and mammals, the situation for squamates, represented today by living species approaching that of birds, some 9000, had until recently remained elusive, and it had been assumed that lizards and snakes were little affected by the event. Squamate history extends well into the deep Mesozoic with crown squamates appearing in the Jurassic and lizards and snakes undergoing their major adaptive radiation in the Cretaceous, with most groups, including iguanids, anguids, geckos, skinks, platynotans and many snake lineages having appeared by the Late Cretaceous. The latter clade of Late Cretaceous lizards, the Polyglyphanodontia comprised some 40% of Maastrichtian diversity. Yet, with the exception of mosasaurs, giant marine varanids of the Cretaceous, major squamate groups were generally thought to have survived the end-Cretaceous extinction event.

Longrich and colleagues, following a revision of fossil squamates from the latest Cretaceous and Paleocene of North America, showed contrarily that both lizards and snakes suffered a devastating extinction that coincided with the Chicxulub bolide impact (Longrich et al., 2012). Their results indicated that the K–Pg event resulted in the elimination of many lizard groups and increased morphological disparity; species level extinction was 83%. Surviving taxa were of small body size and probably large geographic range; the recovery was prolonged, and pre-extinction diversity was not achieved until about 10 million years after the extinction event. Earliest Paleocene diversity is roughly one-third that of late Maastrichtian diversity, and squamates, like birds, paralleled mammals in their rapid adaptive radiation. Squamate diversity does not approach Maastrichtian levels until the early Eocene, coincident with late Paleocene–early Eocene thermal maximum (PETM, Jardine, 2011), some ten million years following the mass extinctions, so biota would be exposed to still another dramatic environmental perturbation (Lindow and Dyke, 2006). As a general pattern the extinction of lizards and snakes, groups predicted to have a good chance of surviving the extinction event, shows that the end-Cretaceous mass extinction was far more severe than previously thought. Longrich and colleagues note that this extinction and reorganization of squamates following the K–Pg boundary underscores the role played by such extinction events in driving diversification (Longrich et al., 2012).

3.5. *Mammals and birds*

Resistance to the view that birds suffered a catastrophic demise at the K–Pg boundary is surprising. The proposed 'burst' or 'big bang' model for avian and mammalian evolution followed discussions between AF and Berkeley biochemist Allan Wilson in the 1970s when Wilson and colleagues were finding amazingly small differences between living orders in amino acid profiles. In the 1980s Wilson and colleagues published papers on bird evolution (Prager and Wilson, 1980; Wyles et al., 1983:4396, 4395), noting that, "A short time scale … has the merit of helping to account for the small molecular differences observed among modern birds,"(4396), and, "the time scale for evolutionary divergence of modern birds could be quite short … the possibility that the lineages leading to all modern birds stem from … ancient bird species that lived about 65 million years ago … deserves attention" (4395). While enthusiastic support came at the time from paleontologists, resistance from groups in the ornithological community was substantial, largely because of the lure of explaining modern avian distribution of flightless birds by drifting continents, vicariance biogeography (Cracraft, 1973). Today little has changed, but the debate centers more on molecular vs. paleontological (clocks vs. rocks) data; but new avian evidence from the Eocene of the Northern Hemisphere in particular has added tremendously to our knowledge of Paleogene bird evolution (Feduccia, 1999; James, 2005; Mayr, 2005, 2009; Lindow and Dyke, 2006; Dyke and Lindow, 2009; Lindow, 2011; Grande, 2013).

Mammals and birds are discussed together because debate concerning the timing of the ordinal diversification and evolution of modern forms is closely parallel. In both cases estimates of time of origin based on molecular clocks approaches a span of 145–65 million years, nearly the duration of the Cretaceous Period (Wible et al., 2007). Most molecular approaches date the origin as far back as the Early Cretaceous, around 100–120 Myr. In contrast, paleontologists typically view the origin at the end of the Cretaceous or the early Paleocene, the result of a massive reorganization following Cretaceous extinctions (Feduccia, 1999, 2003). For mammals such a scenario would place these divergences before or shortly after the appearance of eutherians in the fossil record (Archibald, and Deutshman, 2001). The same exact scenarios appear in the avian literature, where the first appearance of archaic ornithurine birds in the Early Cretaceous approximates the molecular clock estimates for divergence of modern neornithine orders, but contrarily an explosive post-K–Pg radiation is undeniably seen in the fossil record, regardless whether some few lineages passed through the extinction bottleneck.

These interpretations tend to be bolstered by continued citation of misleading papers that cannot be easily tested and linger in the literature. Some estimates of divergence times are astounding, with some systematists using molecular clocks to suggest divergence of whales (Cetacea) from other mammalian orders in the Early Cretaceous (Hedges et al., 1996), while fossil evidence is clear on a post-Cretaceous origin (Alroy, 1999; Novacek, 1999; Gingerich, 2006), probably within 8–10 million years following the Cretaceous extinctions (Thewissen and Bajpai, 2001). Specifically, the origin of the Archaeoceti (hence Cetacea) is constrained to about 54–55 Myr (beginning of Eocene), while the divergence from Artiodactyla was likely as early as 64–65 Myr (beginning of Cenozoic) (Bajpai and Gingerich, 1998). Although such constrained dates for the origin of avian orders are lacking, we do know that the large flightless birds of the genus *Gastornis* (*Diatryma*), possibly of gruiform or anseriform ancestry, were present by the Paleocene of Europe and became extinct by middle Eocene there and presumably in North America and Asia (Mayr, 2009), thus representing a rapid avian origin and extinction. Like the mammal paleontologists, those studying avian fossils are also sharply divided on the tempo and mode of bird evolution, with one group favoring the explosive 'burst' model with a K–Pg bottleneck from a Late Cretaceous phylogenetic fuse (Feduccia, 1995, 1999, 2003), and those supporting origins of modern birds deep in the Cretaceous at 100 Myr or even older based on molecular clocks and hypothetical vicariance biogeography, even though solid fossil evidence with constrained dates is lacking.

Although actual origins should logically precede fossil finds, the postulation of 'phylogenetic fuses' or ghost lineages does little to advance our knowledge, so to state that both origins and diversifications lie deep within the Cretaceous (Hedges et al., 1996; Cracraft, 2001a; Dyke and Van Tuinen, 2004) does little more than confuse the issue. Going back, Cracraft (1986) proposed a Cretaceous origin of the Neornithes based on incorrectly identified fossils, but supported by his phylogenetic analysis. However, by combining known fossil data of three clades (Strigiformes, Caprimulgiformes, and Apodiformes) within a statistical fossil gap analysis, Marshall (1997) and Bleiweiss (1998) showed a likely origin within a short time during the early Paleocene. What both molecular and morphological studies have largely ignored is the necessity of distinguishing between a putative time of origin of a group and its diversification (Dyke and Van Tuinen, 2004; Van Tuinen et al., 2006), the latter being the important factor in an evolutionary and ecological sense (Alroy, 1999).

The same is largely true for the fossil record of mammals, and there is still no evidence for any modern placental or marsupial in the Cretaceous, either postulated from ghost lineages or from actual fossils (Novacek, 1999; Rose, 2006). Recently, O'Leary and colleagues took a fresh approach to the timing of the mammalian radiation by scoring 4541 phenomic characters for 86 fossils and living species. When their data were combined with molecular sequences, they produced a phylogenetic tree that, when calibrated with fossils, showed placental orders originating after the K–Pg boundary (O'Leary et al., 2013; Yoder, 2013); the result was in contrast to the clock-supported view of some 29 mammalian lineages (including stem primates and rodents) appearing in Late Cretaceous ecosystems and surviving the K–Pg extinction event (Meredith et al., 2011; Murphy et al., 2001). The same exact scenarios based on molecular clocks have been proposed for birds, beginning in 1997 (Cooper and Penny, 1997). However, Graur and Martin (2004:80) correctly point out that the early divergence-time estimates are based on single calibration points and tenuous methodology, and the entire venture of estimates based on putative molecular clocks may be in error by a huge margin. Most disturbingly there is no definitive yardstick against which they can be checked (Pulquerio and Nichols, 2006). Gingerich lamented that if 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" (Gibbons, 1998:676). Many of the clock studies suffer from

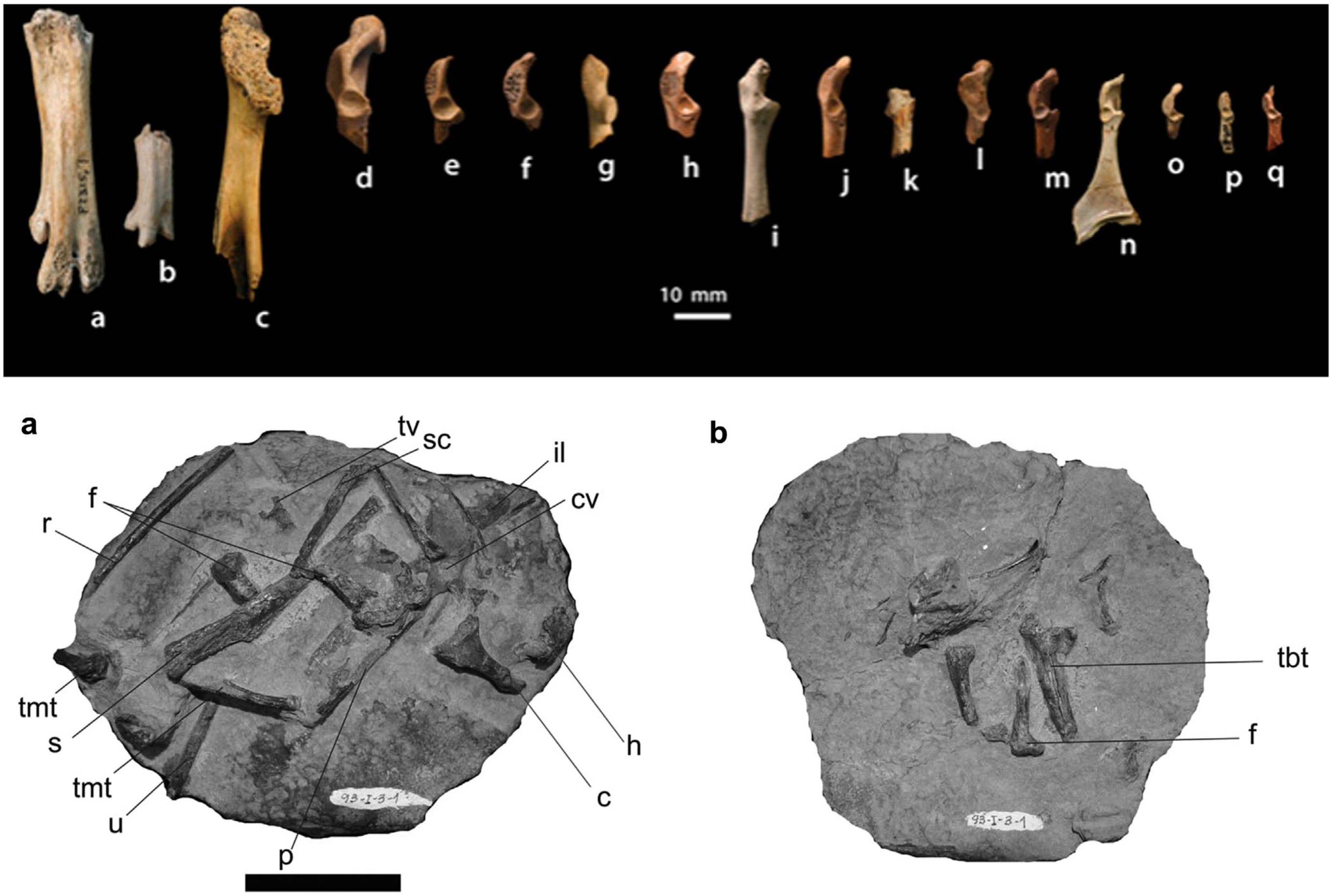


Fig. 2. Late Cretaceous scrappy bird fossils. Upper image, late Maastrrichtian fossils Showing size range. Hesperornithiform A; B, Hesperornithiform B; C, cf *Avisaurus archibaldi*; D, Ornithurine C; E, Ornithurine F; F, *Cimolopteryx maxima*; G, Enantiornithine A; H, *Ceramornis major*; I, Ornithurine D; J, Ornithurine B; K, Enantiornithine B; L, *Palintropus retusus*; M, Ornithurine A; N, *Cimolopteryx rara*; O, *Cimolopteryx petra*; P, Ornithurine E; Q, *Cimolopteryx minima*. Below, the putative modern duck *Vegavis*, from Antarctica: (a). half of the concretion preserving most of the skeleton of the holotype; (b) other half of the concretion with few bones. Abbreviations: c, coracoids; cv, cervical vertebra; f, femora; h, humerus; il, ilium; p, pubis; r, radius; tmt, tarsometatarsus; tv, thoracic vertebrae; s, sacrum; sc, scapula; u, ulna (scale bar 50 mm). Upper courtesy N. Longrich and Proceedings of the National Academy of Sciences (from Longrich et al., 2012. Mass extinction of birds at the Cretaceous–Paleogene (K–Pg) boundary. Proceedings of the National Academy of Sciences 108(37), 15253–15257); lower from Reguero et al., 2013; reproduced with permission though Geological Society of London guidelines.

improper calibration and inadequate sampling of taxa, and another problem involves making inappropriate comparisons. As an illustration, Paton et al. (2002), rejected a rapid Paleogene avian radiation hypothesis and a "transitional shorebird" ancestry based on mitochondrial DNA sequences of the highly derived crown-group shorebirds, turnstone (*Arenaria*) and oystercatcher (*Haematopus*), taxa no more allied with the long-extinct and hypothetical construct of "transitional shorebirds" than any other modern bird.

If the explosive model is incorrect for birds and mammals, how is it that virtually all modern placentals (primates, bats, ungulates, whales, etc.) [and neornithine birds] "appear so abruptly in the fossil record?" (Yoder, 2013:656), and no representatives of modern mammalian placentals are known from the Cretaceous (Novacek, 1999; Rose, 2006). Part of the confusion may arise from the presence of a few modern lineages back in the Cretaceous, but "The fact that there was an early Cenozoic mammalian radiation is entirely compatible with the existence of a few Cretaceous splits among modern mammal lineages" (Alroy, 1999:107).

4. Fossil birds near the K–Pg boundary

There has been considerable attention given to a small but diverse collection of bird bones of ornithurine, and possibly neornithine affinity, from North America, most recently reexamined by Longrich and colleagues (Fig. 2). These bones come from three formations: Hell Creek of Montana, North and South Dakota, Lance of Wyoming, and Frenchman of Saskatchewan. Although largely single bones, the fossils take on particular importance as they come from the final 1.5 million years of the Cretaceous and most are within 300,000 years of the K–Pg boundary (Longrich et al., 2011; Hicks et al., 2002).

Many of these isolated bones have over the years been shoehorned into modern orders based on overall similarity, but given the degree of mosaic evolution expected at that time, such identifications are truly precarious and suspect, especially for calibrating molecular clocks (Marsh, 1892; Brodkorb, 1963; Hope, 2002). Nevertheless, a pattern has emerged with several genera of putative charadriiform affinity, namely *Cimolopteryx* and *Palintropus* (possibly closely allied with *Apsaravis*, Longrich, 2009). Longrich and colleagues assembled a collection of most of these fossils and, using phylogenetic analysis, concluded that a total of 17 species are represented, including 7 of archaic avian types, including Enantiornithes, Ichthyornithes, Hesperornithes, and an *Apsaravis*-like bird, none of which are known to have survived into the Paleocene. They conclude that their presence into the latest Maastrichtian provides substantial evidence for a mass extinction of archaic birds coinciding with the K–Pg event and therefore with the Chicxulub asteroid impact. However, of the remaining birds most represent advanced ornithurines, and given their diversity, represent a major radiation of Ornithurae that preceded the end of the Cretaceous. Importantly, although these fossils may well represent neornithines, given their scrappy nature, none can be definitively referred to Neornithes, and the authors refer to them as derived Ornithurae (i.e., birds closer to Neornithes than to *Ichthyornis*), but assert that "the available material is inadequate to determine whether any of these species are members of Neornithes as previously asserted…, or whether they fall outside the clade."

The most abundant and morphologically diverse of these birds is the genus *Cimolopteryx*, with species ranging in size from that of a very small, to a large gull. The fossils show that, like the enantiornithines, ornithurines by Late Cretaceous had evolved diverse body sizes. The larger *Avisaurus* and Ornithurine C (of Longrich et al., 2011) are roughly 5 and 3 kg, respectively, and among the largest volant forms of the Mesozoic; and surprisingly, very large birds (~10 kg) are conspicuously absent, perhaps unable to penetrate the niche occupied by large pterosaurs. Also included among the Lancian birds are the genera *Lonchodytes*, *Graculavus*, *Potamornis* and an unidentifiable piece of lower jaw from a supposed parrot-like bird, but is not allied in any way with modern parrots and may not be avian. Most, however, have been variously referred to the Charadriiformes, based on dubious criteria, and many characters utilized may represent plesiomorphs; nonetheless, it is notable that in many respects they are osteologically congruent with Charadriiformes, and an additional avian specimen reported from the Upper Cretaceous of Antarctica was referred to the family Burhinidae, considered a basal charadriiform, suggesting possible affinity to the cimolopterygids (Cordes, 2002). Dyke and colleagues (2002) reported on a large ornithurine from the Maastricht Formation of Belgium, close to the K–Pg boundary, at 65.8 Ma. The fossil is the youngest non-modern bird known anywhere in the world, and it is clearly a non-neornithine, close to *Ichthyornis*.

In summary, the study by Longrich, Tokarky and Field found that rather than disappearing gradually over the course of the Cretaceous, minimally four lineages of archaic birds, Enantiornithes, Hesperornithes, Ichthyornithes and Apsaraviformes (Palintropiformes), persisted up to the K–Pg boundary, and no archaic birds have ever been reported from the Paleogene. They also found, surprisingly, that although enantiornithines are commonly referred to as the dominant landbird lineage of the Mesozoic, the assemblage is dominated by ornithurines, many representing advanced but archaic ornithurines (i.e. closer to the crown than to *Ichthyornis*). They thus significantly document for the first time a major radiation of advanced ornithurines, some possibly neornithines, before the end of the Cretaceous.

This study takes on particular significance in that these North American latest Cretaceous fossils can be stratigraphically constrained to the final part of the Cretaceous. Outside of North America the situation is far from satisfactory in this respect, and although a wide array of archaic birds are known from the Late Cretaceous of Asia, Europe, South America (including Antarctica), and Madagascar, many lack any temporal constraint; and those that do have nice stratigraphic control, are based largely on single or scrappy elements. A recent example of problematic stratigraphy involves beautifully preserved massive trackways of shorebirds from what was called the Late Triassic Santo Domingo Formation (published in *Nature* in 2009 and cited in Feduccia, 2012), but which turned out on to be some 175 million years too early, and are in reality late Eocene (Melchor et al., 2013).

Examples of scrappy material entering the literature abound; for example, Kurochkin reported the presence the modern procellariiform family Diomedeidae in the terminal Cretaceous on the basis of a clavicular splint (Kurochkin, 2005), and a "presbyornithid" also based on scrappy material (Kurochkin et al., 2002). Hope (2002) noted that the supposed modern procellariiform specimen was "consistent with the determination." Such unwarranted assessments confuse the record and should not be published. Another problematic fossil is a Late Cretaceous putative modern duck *Vegavis* (Anatidae) reported from Antarctica by Clarke (Clarke et al., 2005; Fig. 2, lower) in Nature as the first "definitive" evidence of the extant avian radiation in the Cretaceous. One of two fossils was earlier identified as a presbyornithid (now *Vegavis*), the other a loon (Noriega and Tambusi, 1995), the latter being questioned or disputed (Mayr, 2004; Mayr et al., 2013; E. N. Kurochkin, 2001, pers. commun. from study of specimen in 1992: "bones are absolutely not gaviiform … It is not a loon"). Yet, identification of this scrappy material referred to "modern duck" and "loon" is not satisfactory, especially for such dramatic finds. The putative duck fossil has little in the way of any anseriform signal in the postcranial skeleton, and although it exhibits a complex hypotarsus typical of some neornithines, the evidence for a sister group relationship to Anatidae is highly ambiguous. The identification is based on a single character, the presence of three hypotarsal furrows for deep flexor tendons. Mayr, however, notes that an identical hypotarsus is known from stem group gaviiforms (*Colymboides*), and *Colymbiculus*, as well as the phoenicopteriform *Palaelodus*, and has thus evolved at least three independent times (Mayr, 2013). Aside from the hypotarsus, other skeletal morphology of *Vegavis* is quite different from that of Anatidae and Anseranatidae, so additional evidence will be necessary to accept this identification and *Vegavis* must remain at present as incertae sedis. Too, there is considerable lower Eocene strata in the region and more exploration is needed to fully constrain the temporal context of these fossils and eliminate the possibility of reworking of sediments, or persistence of resistant fossil-containing nodules from other strata. A further complication for the identification of any Late Cretaceous bird is the restriction of osteological comparisons of the fossil to modern taxa which may not be appropriate. This putative duck fossil is particularly problematic since it is being used to calibrate molecular clocks (Jetz et al., 2012), with obvious disastrous consequences. Clarke, for example, notes that "We know from *Vegavis* that there had been several major splits in the radiation of living birds by the latest Cretaceous," (quoted in O'Donoghue, 2010), and therefore derives support for an origin of modern birds about 100 million years ago; yet there is absolutely no fossil evidence for such a claim.

While the North American avian fossils studied by Longrich and colleagues may not allow inference of a K–Pg mass extinction of birds, they are consistent with such a proposal, and are likely indicative of a worldwide extinction event. Lindow cited selective evidence suggesting that non-neornithine birds were declining in diversity or had disappeared before the end of the Maastrichtian (Lindow, 2011), but there is evidence to the contrary, especially from a diverse Late Cretaceous fauna from Saskatchewan (Tokaryk et al., 1997); and enantiornithine and hesperornithiform fossils are known in the latest Cretaceous (Longrich et al., 2011). In another study, Martin and colleagues described an entirely new lineage of hesperornithiform diving birds, family Brodavidae, consisting of a single genus and four species form the Late Cretaceous (Maastrichtian) of Asia and North America. Included in the family are the latest records of the order Hesperornithiformes, representing the first freshwater species, some possibly with volant abilities (Martin et al., 2012). The absence of identifiable members of modern orders shows that the latest Cretaceous avifauna in North America was still far from modern. This evidence is fully consistent with a major extinction of archaic birds at the K–Pg boundary, which was followed by rapid radiation of modern birds in the Paleogene.

One can speculate on what types of birds may have somehow survived the impact event (Feduccia, 1995, 2003; Robertson et al., 2004; Lindow, 2011). Dyke and colleagues (2007:339), noted that (in contradiction to Paton et al., 2002), "paleontological data supports a "shorebird" or "waterbird" transition in prevailing environments of preservation in the aftermath of the K–P extinction," citing evidence indicating that only 7% of named birds from early Paleogene are from terrestrial sediments, and nearly 90% are from lacustrine or marginal marine sediments, regardless of preservational potential. This view also conforms to the predominance of the shorebird-like dominant cimolopterygids in the Late Cretaceous, the ability of other waterbirds to obtain food, and the ability of some such as living penguins and shearwaters to excavate burrows. Too, judging from modern counterparts many birds, ranging from poorwills and todies to hummingbirds, and even vultures, are capable of lowering body temperatures and undergoing varying states of torpor, and this physiological phenomenon may have been more prevalent during the Late Cretaceous in archaic ornithurines. It has been suggested before that birds such as volant paleognaths and perhaps shoreline detrital feeders might be good candidates for survival (Feduccia, 1995; Janzen, 1995). With their rhynchokinetic skulls lithornithids may have used their long and narrow beak for probing along shorelines or other waters (Houde, 1988; Houde and Olson, 1981); they therefore fit the bill for birds that may have somehow survived the K–Pg cataclysm and passed through the bottleneck. Small, volant paleognaths, perhaps with burrowing habits (like modern coraciiforms, shearwaters and penguins, etc.), and torpor, may have stood a reasonable chance of survival. Kiwis are burrow-builders (often building numerous burrows), and the Stewart Island kiwis emerge at night to probe for invertebrates and other food in the beach sand (personal observation). They may have been omnivorous, or capable of detrital, shoreline probe feeding. Living basal shorebirds such as crab plovers and burhinids, or their kin, might also be survival candidates, in addition to divers, filter-feeding waterbirds such as anseriforms, and even galliforms that are primarily granivorous; but this is all speculation. Yet, survival of a few major lineages in no way negates an explosive model for the Paleogene avian radiation and a K–Pg bottleneck.

5. Discussion

There is little question that many avian groups, including opposite birds or enantiornithines, and archaic ornithurines (including hesperornithiforms and ichthyornithiforms), became extinct at or near the K–Pg boundary, along with myriad vertebrates and the volant pterosaurs which were to some extent Mesozoic avian competitors. The diverse Enantiornithines, predominant Mesozoic landbirds ranging from sparrow- to vulture-sized birds, were abundant worldwide during the Late Cretaceous (Chiappe and Dyke, 2002), and are assumed to have become extinct with the archaic ornithurines, which at least from Early Cretaceous evidence were largely water- or near-water denizens, ranging from the grebe-like *Gansus* to the more typical shore-dwellers, and forms such as *Apsaravis* (Mongolia) and *Limenavis* (Argentina). We can conclude that archaic members of the Ornithurae were widespread and successful avifaunal components of the last stages of the Mesozoic but absent after the end-Cretaceous extinctions. There is one problematic Chinese early-mid Paleocene species *Qinornis paleocenica* which shows possible affinity with the Late Cretaceous non-neornithine *Apsaravis*, and may suggest some basal ornithurines survived across the K–Pg boundary (Mayr, 2007), but it is certainly exceptional. No crown clade ornithurines have yet been recovered, if indeed they were present (Mayr, 2013).

Recently discovered New Zealand penguin fossils comprise four naturally associated skeletons from a Paleocene formation just above a well-known Cretaceous/Paleogene boundary site. Fossils of this new genus *Waimanu* provide a lower estimate of 61–62 Ma for the divergence between penguins and other birds, and it is possible that penguins will be found even earlier, some undescribed penguin-like fossils having been discovered from putative latest Cretaceous deposits on Chatham Island (Hansford, 2008).

The fossil record is clear that there was not "mass survival" of neornithine birds across the Cretaceous boundary, as originally suggested by Cooper and Penny (1997). Yet, another recent study using mitogenomic analysis concluded that modern birds originated by mid-Cretaceous with at least 22 lineages crossing the K–Pg boundary (Pacheco et al., 2011), but there is no fossil evidence to support these dates. Some of these estimates range from roughly 100 million years to 120 for the split of Palaeognathae–Neognathae and Galloanserae–Neoaves, to 110 for a primate-rodent split, and 82–85 for origin of Passeriformes (Feduccia, 2003). Among the more recent studies are from Ericson and colleagues (2006, 2014) who attempt integrating molecular sequence data and fossils. They conclude (p. 543) that their calibration suggests that "Neoaves, after an initial split from Galloanseres in Mid-Cretaceous, diversified around or soon after the K/T boundary." … but they also found no solid molecular evidence for an extensive pre-Tertiary radiation of Neoaves.

In still another study inferring evolutionary trees from complete mt genomes to attempt to resolve deep Neoavian splits (using conclusions of Cracraft (2001a,b) as testable starting points or "priors"), Pratt and colleagues (2008:322) conclude that "at least 12 Neoavian lineages had evolved prior to the K–Pg boundary." At another extreme, Graur and Martin (2004) argue that estimates on molecular clocks are notoriously unreliable, and that, combined with use of unreliable fossils render the entire venture highly speculative. However, based on the single scrappy specimen of *Vegavis*, Clarke and colleagues (2004) estimate that a minimum of five modern lineages originated deep in the Cretaceous, including duck, chicken and ratites. Given the unreliability of Late Cretaceous scrappy fossils to date (Hope, 2002; Clarke et al., 2005; Chiappe, 2007), we are in the dark on possible pre-K–Pg origins of Neoaves, either from fossils or the molecular clock data, and there is really no outside check for verification at this point.

Abrupt appearance of the major groups of both birds and mammals following the K–Pg boundary, within a period of 2–8 million years, has been suggested before as the primary reason that varied systematic methodologies ranging from classical to phenetic, cladistic, and molecular, have so far failed to produce a verifiable phylogeny (Feduccia, 1995, 1999, 2003). Most methodologies appear quite reliable for generic relationships, but become more and more unreliable as one ascends to the family, and especially the ordinal level. If these orders are splitting off their phylogenetic nodes in this remarkably short time period, then it would imply an explosive radiation, and it would be virtually impossible to detect precise higher level relationships. Similar conclusions have been reached by any number of recent workers. For example, Poe and Chubb (2004) suggested that the large polytomy at the base of the Neoaves radiation signals a rapid radiation that "might be considered simultaneous." (see also Fain and Houde, 2004). Poe and Chubb suggest that despite over a century of effort in all branches of avian systematics, a robustly-supported avian phylogeny has not been achieved. The reason may be that the avian evolutionary pattern may violate the assumption of a dichotomously branching tree, and their "bush" result from five independent gene trees examined indicates an explosive evolution in the early Paleogene, the avian tree representing a simultaneous radiation of multiple lineages, producing extremely short branches or internodes for interordinal relationships and therefore unresolvable phylogenies.

5.1. Gondwana genesis

A model for an ancient origin of birds, still popular today, cites continental breakup in a manner of classic gradualism, by which: a) the origin of modern birds was influenced mainly by the dispersal of the southern continents and occurred mainly in Gondwana, and b) numerous neornithine lineages arose prior to, and passed through, the K–Pg extinction event. This model can no longer withstand any level of serious scrutiny, as its poster child, the flightless ratites, are completely unknown prior to the Paleogene; and small, volant tinamou-like palaeognaths, the lithornithids or stone birds, putative ratite ancestors, are found abundantly in the Paleocene and Eocene of the Northern Hemisphere. These birds were fully capable of dispersing by air to various land masses, including New Zealand and Madagascar, following the continental breakups, and independently giving rise to varied flightless descendants. New phylogenomic evidence for multiple loss of flight in varied ratites suggests at least three independent losses of flight, and "demands fundamental reconsideration of proposals that relate ratite evolution to continental drift"(Harshman et al., 2008).

Instead of an ancient origin, flightlessness is a common phenomenon in birds, with flight having been lost in 18 extant families, innumerable times within the Rallidae (Steadman, 2006; Feduccia, 2012), and gigantism can quickly evolve in the absence of anatomical constraints for flight architecture. The now classic example involves the extinct grazing goose-like ducks or moa-nalos (*Thambetochen*, etc.) of the Hawaiian Islands, a group that probably evolved within a few million years to sport a postcranial skeleton closely resembling the ratites in many skeletal features (Olson and James, 1991).

There is a possible large putative paleognath from the upper Paleocene of the Paris Basin, but regrettably it is based solely on an anterior thoracic vertebra (Buffetaut and Ploeg, 2008), and cannot be identified with any certainty. The oldest known demonstrable ostrich, moa and elephantbirds are lower Miocene, Pliocene, and Plio-Pleistocene, respectively (Feduccia, 1999; Mourer-Chauviré et al., 1996). In addition, a large French Late Cretaceous flightless bird *Gargantuavis* is definitively not a ratite (Buffetaut, 2002). There is no longer any evidence to support an ancient origin of any living ratites, and Thomas Huxley's 1867 view of ratites as 'waifs and strays' of an ancient avian Mesozoic radiation is no longer tenable (Feduccia, 1999). Among the most significant Paleogene fossils related to this issue are the lithornithids, volant palaeognathous birds, ranging from turkey-sized to much smaller, from the Paleocene/Eocene of the Northern Hemisphere (Houde and Olson, 1981). With their rhynchokinetic skulls stone birds may have used their long and narrow beak for probing along shorelines or other waters (Houde, 1988); they are therefore candidates for birds that may have somehow survived the K–Pg cataclysm and passed through the bottleneck. In contrast to the morphologically similar tinamous, lithornithids were probably strong flyers capable of sustained flight, and had a long hallux and curved ungual phalanges, indicating good perching ability. They would have been fully capable of crossing water barriers and giving rise to flightless ratites.

The theme of a Gondwana genesis of many neorithine lineages, pioneered by Cracraft (2001a,b), still gains support by some authors (including Boles, 1995, and Edwards and Boles, 2002, for passerines), but is not supported by any fossil evidence. Yet, it is still promoted in the literature and prominently on display in text books, and therefore deserves continued discussion. Cracraft's arguments were based on minimum ages of lineages from vicariance events from the geological data, and he used current distributions to pattern the biogeographic events. His claim was 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…".

However, it is imperative to consider the continental configurations as they were shortly after the K–Pg extinction event, when the southern continents were drifting apart but were not at the current distance of some 2600 km of trackless ocean now separating South America from Africa (Fig. 3). As late as 50 Ma the shortest distance between Africa and South America was approximately 1000 km from present day Sierra Leone to Paraíba state, Brazil (De Oliveira et al., 2009); this is the present-day distance from the coast of Ecuador to the Galápagos Islands, which are inhabited by some 24 endemic species, and some 19 species of seabirds (5 endemic) with some 750,000 seabirds on the islands. The existence of considerable extensions of dry land in the South Atlantic before 40 Ma has been postulated, possibly stretching some 500 km into the Atlantic, reducing migration distance in the late Paleocene/Eocene, and combined with a known volcanic island arc along the Mid-Atlantic Ridge, would have greatly facilitated island hopping; the same may be true for some mammal groups, "reconstructions of South Atlantic geometry, palaeowinds and palaeocurrents during the middle Eocene … are consistent with trans-Atlantic sweepstakes dispersal of caviomorph rodents and platyrrhine primates from Africa to South America" (Antoine et al., 2012; De Oliveira et al., 2009; Poux et al., 2006). Most important, evidence of representatives of extant pantropical birds, such as trogons, todies, motmots, hoopoes, mousebirds, stem rollers, oilbirds and frogmouths, parrots, and others, now known from Northern Hemisphere Cenozoic fossils have been discovered during the past three decades (Mayr, 2009). These myriad groups were driven to their current pantropical distributions following late Cenozoic climatic deterioration in the higher latitudes, therefore falsely giving the impression that these groups originated on a single Gondwanan continent before the breakup (Feduccia, 1999, 2003). When one constricts and overlays today's major migration routes on an early Eocene map of the continents (Fig. 3), with the expansive distribution of numerous extant birds (Fig. 4) it is difficult to argue for a vicariance model for avian biogeography.

By any measure rails are considered "weak" fliers, with a relatively small percentage of total body weight devoted to the flight apparatus; yet, they are among the most widespread of all avian families, and capable of extraordinary long migrations over land and extensive stretches of ocean. They have colonized almost all the South Pacific islands, and the purple swamphen (*Porphyrio porphyrio*), ranges from the Mediterranean basin and Africa across parts of Asia, on to Australia and New Zealand. Consider the migration of the shining bronze cuckoo (*Chrysococcyx lucidus*), which traverses some 3200 km of ocean from its breeding grounds in New Zealand to its winter range in the Solomon Islands (Fig. 3, lower right).

Although there is compelling evidence against a model of a Gondwana genesis and distribution of flightless ratites, the vicariance model for avian distribution in the Late Cretaceous persists; and appeal of the vicariance model was so enticing that Dawkins devotes 15 pages in his book *The Ancestor's Tale* (Dawkins, 2004), to the currently popular model, telling us: "The ratites reached their present separated homelands without benefit of flight. How did they get there? … They walked. All the way…".

5.2. *Mosaics abound*

A problem not receiving sufficient attention is the well-known phenomenon of mosaic skeletal evolution seen in complete skeletons of Paleogene birds which do not fit neatly into any modern order (Feduccia, 1999, 2003). Examples abound, but among the more vivid are: a) *Rhynchaeites*, variously described as a shorebird-gruiform, a shorebird, and later shown to fit best as an ibis once the skull was known; b) *Juncitarsus*, which has a tarsus virtually

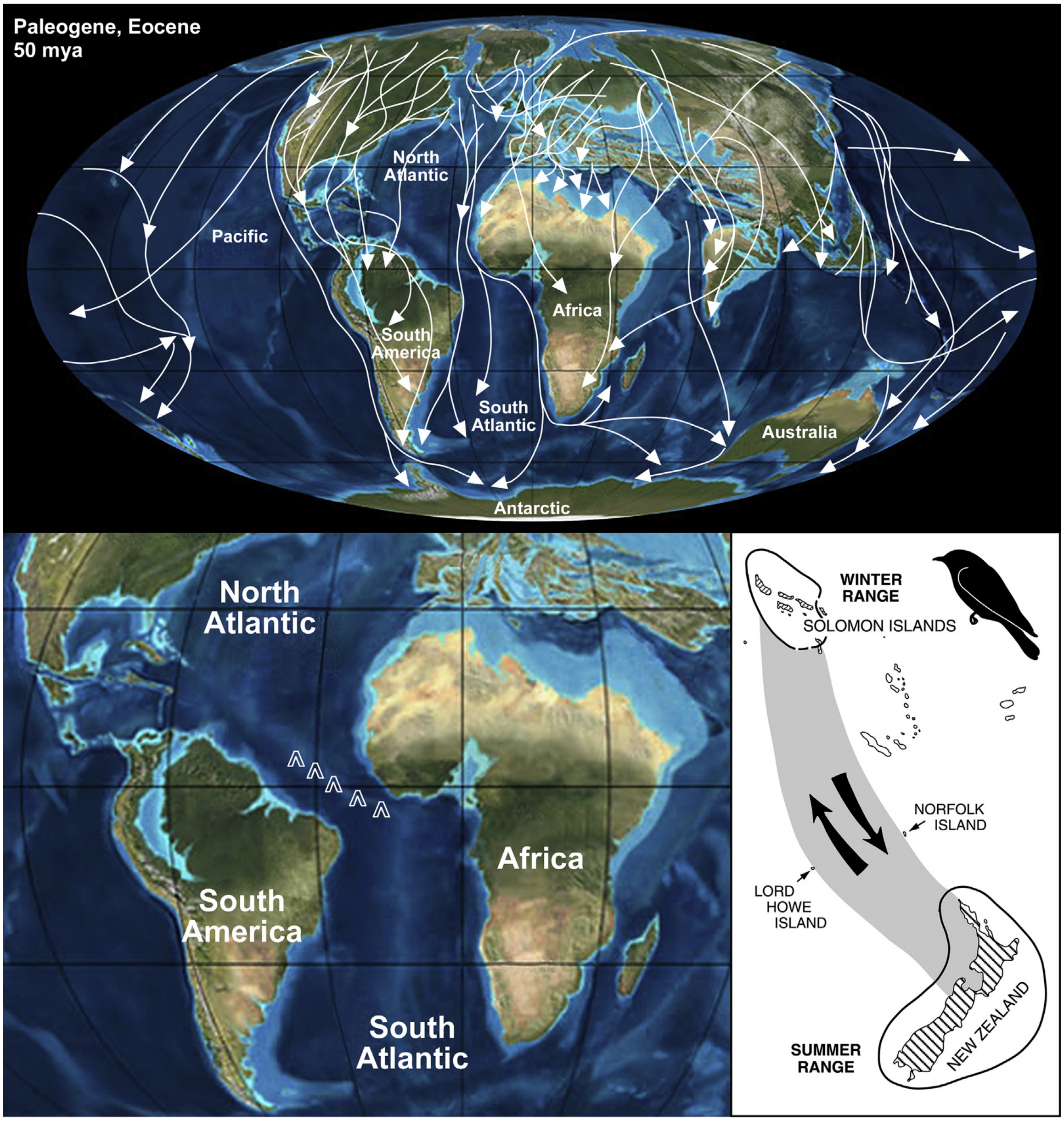


Fig. 3. Map of the world during the Paleocene–early Eocene (approx. 50 Ma) showing the proximity of South America and Africa with the zipper-like volcanic arc of the Mid-Atlantic Ridge, the world's largest mountain range, with some of today's major avian migration routes constricted and overlayed. Volcanic islands in the South Atlantic today include, notably, the Tristan da Cunha group, including Tristan da Cunha, Inaccessible Is., and Cough Is., as well as St. Helena Is. some 2000 km to the north; and its nearest neighbor to the northwest is Ascension Island. Saint Helena is home to an endemic plover, the wirebird (*Charadrius sanctaehelenae*), and the Tristan da Cunha group has some 80 avian species, including six endemics. All have landbirds, which include a variety of flighted and flightless rails (some extinct), as well as finches, thrushes, a warbler, a swallow, nighthawk, kingbird, and a great variety of seabirds, including and the famous Inaccessible Island's flightless rail *Atlantesia rogersi*. None arrived by drifting continents. The same applies to the Hawaiian avifauna and South Pacific oceanic islands. Lower, the same map showing putative volcanic islands along the Mid-Atlantic Ridge, possible way stations for birds between continents. Lower right, migratory route of one geographical race of the shinning cuckoo (*Crysococcyx lucidus lucidus*), which traverses some 3200 km of ocean (much longer than the distance between lower Eocene southern continents), from its breeding grounds in New Zealand to its winter range in the Solomon Islands. (Adapted from Feduccia, 1996). (Maps adapted and modified from: Scotese, C.R., 2002, http://www.scotese.com, (PALEOMAP website), and Paleogeographic map; reproduced under guidelines of Ron Blakey, Colorado Plateau Geosystems, Inc© (http://cpgeosystems.com/index.html).

identical to that of stilts (Recurvirostridae), but with a skull and humerus of a flamingo-like bird (Peters, 1987); c) *Presbyornis*, described in two separate charadriiform families, a flamingo, based on the skull frontal region identical to that of a baby flamingo, but later discovered skulls were similar to primitive algal-feeding ducks (Olson and Feduccia, 1980); d) *Foro*, a landbird with bones that could be described individually as those of a cuckoo, touraco (musophagid), or hoatzin; e) *Limnofregata*, an Eocene frigatebird, with individual bones assignable to booby, frigatebird, or unassignable to any modern group (Olson, 1977:31). Storrs Olson succinctly notes: "The inadvisability of basing higher taxonomic categories of Paleogene birds [much less Cretaceous birds] on fragmentary limb elements … thus becomes evident." While modern cladistic analyses of Paleogene fossil birds have provided a solid framework for future study, the methodology tends to quantitatively average characters rather than examining each bone independently, so that the phenomenon of mosaicism seldom emerges.

Despite dramatic admonitions for caution, as noted above, bone fragments from the Late Cretaceous continue to be shoehorned into

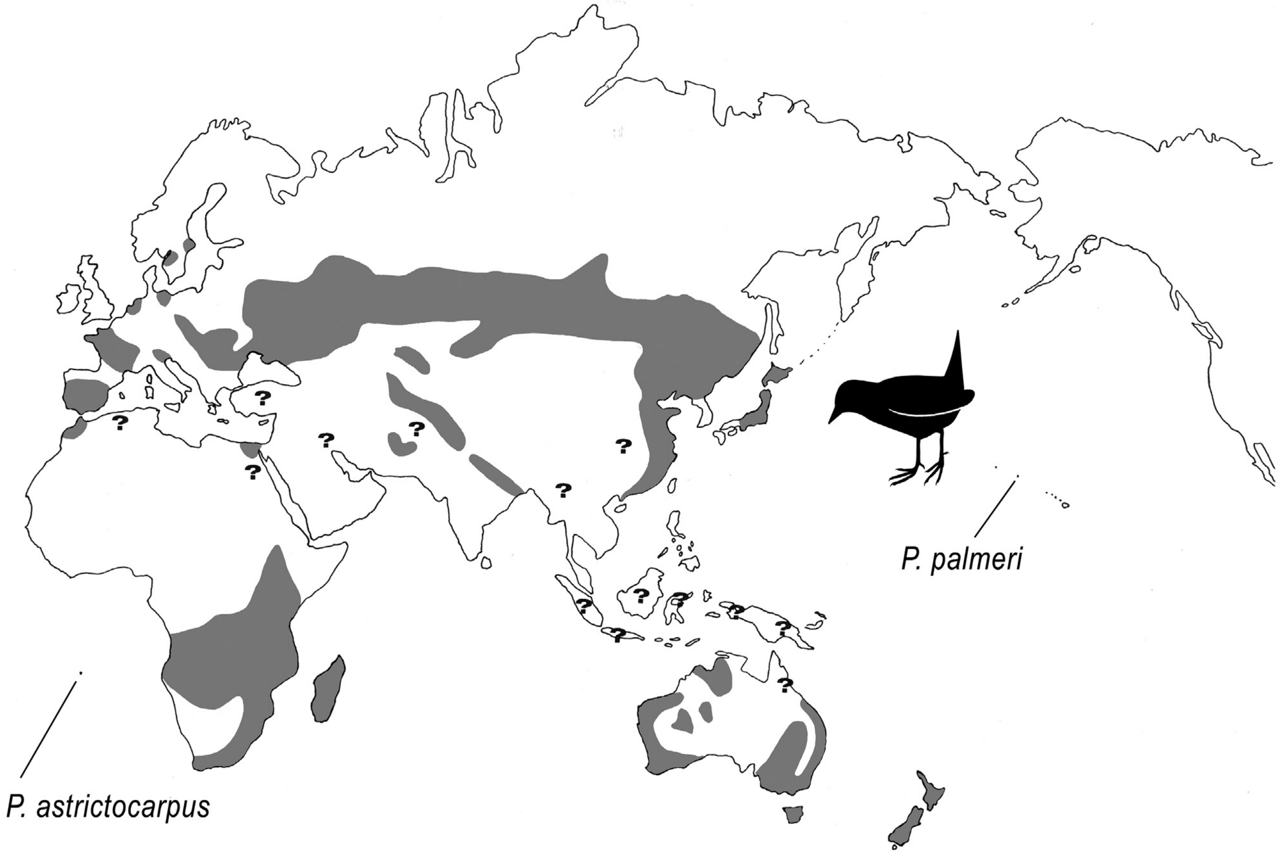


Fig. 4. Map showing expansive distribution of the small rail, *Porzana pusilla*, typical of smaller rails with meager flight musculature, with question marks indicating areas having evidence of prior distribution. Also noted are islands that once were inhabited by two of its derivatives. (Adapted from Olson, 1973).

modern taxa, including a lower jaw fragment assigned to a parrot (Stidham, 1998; refuted by Mayr, 2009), despite the fact that stem parrots known from the Eocene of both Europe and North America lack a parrot-like skull (Mayr, 2009), and the fossil cannot be definitively identified as avian. Too, and most importantly, the putative, but now disputed, identification of a modern duck *Vegavis*, as well as an unidentifiable quadrate assigned to a "stem anseriform" (Elzanowski and Stidham, 2011), has led to massive speculation and molecular calibrations extending modern lineages deep into the Cretaceous. By implication, then, Galliformes, the putative sister-taxon of Anseriformes, and Neoaves, the sister-taxon of Galloanserae, would have to have been present in the deep Cretaceous (Lindow and Dyke, 2006). Given the rampant homoplasy seen in extant neornithines, including but certainly not limited to, multiple origins of: a notarium, amphirhinal condition, palatine process of the premaxilla in passerines, salt glands, zygodactyly, lobate webbing, cnemial crests (of differing embryological origins but similar adult morphology), etc., it is highly inadvisable to attempt to identify and shoehorn scrappy fossils from the early Paleocene, much less from the Late Cretaceous, into modern neornithine taxa, especially given the preponderance of mosaicism seen in the skeletons of Eocene age, which are used as calibrations points for molecular clock studies. Scrappy material should be reported with brevity without naming the taxon and set aside until more material becomes available.

5.3. *The Sacrosanct Galloanserae (fowl and ducks)*

Among the well-accepted features of the avian tree are a basal dichotomy of paleognaths (ratites and tinamous) and neognaths; and a second dichotomy of a clade of ducks and allies (Anseriformes) and landfowl (Galliformes), known as the Galloanserae. These basal dichotomies are supported by virtually all recent molecular studies, but find little support in the fossil record. Absence of any verifiable fossils representing the Galliformes prior to the Paleogene is striking, and possible, but unconvincing galliform affinity has been reported in the Late Cretaceous *Austinornis* (formerly *Ichthyornis lentus*), and *Palintropus* (Mayr, 2009). As noted, the one putative Late Cretaceous modern duck (*Vegavis*: Anatidae) was reported from scrappy material and serious doubt has been raised concerning its true identity (Mayr, 2013). Like the anseriforms, galliformes too have fossils from the Paleogene, and all known fossils, including *Gallinuloides*, *Paraortygoides* and *Chambiortyx*, represent stem clade taxa (Dyke and Gulas, 2002; Mayr, 2009, 2013; Mourer-Chauviré et al., 2013); and there are as yet no definitive crown clade taxa known from Paleogene strata, and no identifiable galliforms prior to the K–Pg boundary. As for anseriforms, there is some meager evidence for presbyornithids prior to Paleogene, and primitive anseriforms such as *Anatalavis* (formerly *Telmatornis*), allied with modern magpie goose, is known from the lower Paleocene Hornerstown Formation of New Jersey, with closely related fossils from the lower Eocene London Clay (Olson and Parris, 1987; Dyke, 2001). Absence of evidence is not evidence of absence, but at some point fossils should have emerged if present, especially those of heavy-boned flightless ratites. Thus, although supported by molecular comparisons, there is little support from the postcranial skeleton or from the fossil record to support the classic lineage of Galloanseres, or its antiquity (Ericson, 2000; Ericson et al., 2001). In conclusion, there is no substantial verification of fossil galliforms, or even paleognaths prior to the K–Pg boundary.

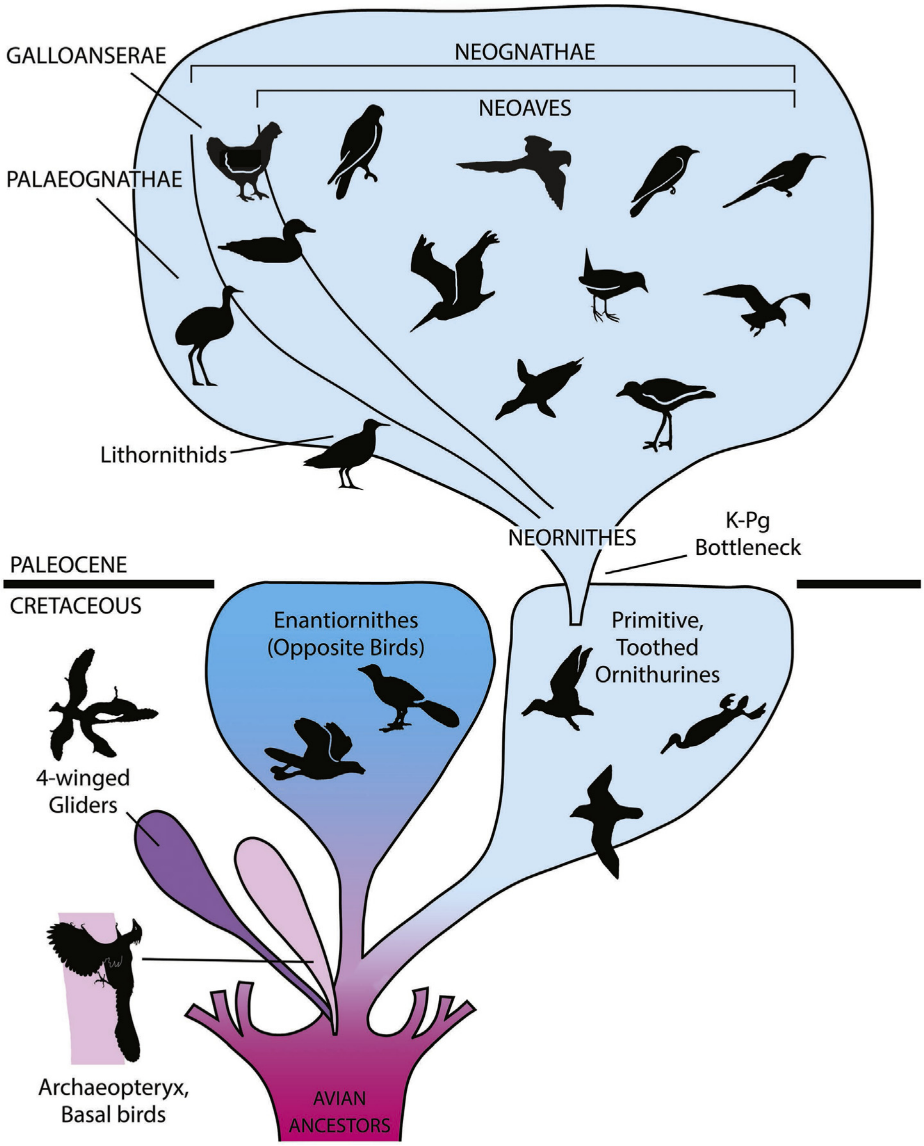


Fig. 5. The Cenozoic 'big bang' model for modern bird evolution, primarily derived from the fossil record, with minimal speculation. (Modified and updated after Feduccia 1995, 2003, and Kaiser and Dyke, 2011).

Questions concerning the currently accepted early phylogeny of birds do not imply it is erroneous, but serve to emphasize that it is a work in progress and great care and healthy skepticism must be exercised to properly ascertain the true phylogeny of birds. Speculation from scrappy fossil material near the K–Pg boundary is not helpful. For example in a major book *Glorified Dinosaurs*, Chiappe (2007) states (and illustrates), "Fossils seemingly pertaining to galliforms, anseriforms, pelecaniforms, gruiforms, charadriiforms . . . procellariiforms … gaviiforms (loons), and psittaciforms (parrots) have been reported from the Late Cretaceous of nearly every continent…," (p. 240), when most are from regions where there is little constraint on stratigraphy, and there is little confidence in the identity of the mostly single bones. He continues, "…the presence of anseriforms in the Late Cretaceous [based on the dubious *Vegavis*] also implies the pre-Tertiary differentiation of both neoavians and paleognaths," and Clarke and colleagues (Clarke et al., 2005) by the same logic implicate a deep Cretaceous divergence of Neoaves with a number of lineages. This is all in stark contrast to the evidence presented in this paper for a massive K–Pg extinction event, which severely affected all vertebrates. How can it be that such an event was not even more severe for birds?

There is hope in the future for a solid phylogeny of birds and mammals based on genomic comparisons, and Hackett and more than a dozen colleagues have constructed an avian phylogeny based on their "phylogenomic" study of 32,000 bases from 19 genes in 169 species (Hackett et al., 2008). In reality, however, they have examined a sample of a relatively small portion of the genome; yet one can find agreement with Scott Edwards that "phylogenomics is our best shot" (Pennisi, 2008:1717). Following Hackett et al.'s phylogenomic study, we can eagerly await the completion of the 10,000 vertebrate genome project, which will produce whole genome sequence for 10 k vertebrates (Haussler, 2009; Hayden, 2009).

6. Conclusions

The case is made for an explosive 'big bang' or 'burst' model for the evolutionary radiation of birds following the K–Pg extinctions, whether caused by multiple factors or a single cataclysmic bolide impact, with a bottleneck allowing a restricted diversity of Late Cretaceous taxa through to the Paleogene, the font of the modern avian radiation (Fig. 5). The early Paleogene explosive model conforms nicely to the typical pattern of evolution: punctuation as a result of massive extinctions, followed by a rapid radiation over an astoundingly short period of time. Extinction typically drives the evolutionary process. Although conflicting molecular clock data consistently argue for a much older origin of birds and mammals with many neoavian lineages as well as placental mammals originating in the Cretaceous at approximately 100 million years or even older, fossil data, written indelibly in the Earth's rocks, and absence of crown-lineage birds in the early Paleogene, argue for a rapid radiation following the K–Pg extinctions. If this hypothesis proves correct and the divergence of most modern avian orders is tightly clustered within a time period of some 5–10 million years, then an explanation would be provided for Stresemann's lamentation of 1959, that we may never fully understand the interrelationships of modern avian orders (Stresemann, 1959).

Evidence, both direct and indirect, argues for an apocalyptic cataclysm that terminated the Cretaceous Period resulting in extinctions beyond our comprehension. It is miraculous that any birds, an environmentally sensitive group, survived. Massive extinctions in birds, mammals and other groups were the driving force for an explosive evolution characterizing the early Paleogene. When confronted by a famous paleontologist skeptical of a cataclysmic K–Pg extinction based on selected survivals, the late Nobel laureate Luis Alvarez responded (and then left!): "…I'm giving you the stars and you're giving me frogs?" (Monmaney, 1993:48–49).

Acknowledgments

I thank Frances James, Zhonghe Zhou and an anonymous reviewer for reading the manuscript and providing suggestions for improvement, and David Kring and Nicholas Longrich for permission for Figs. 1 and 2, respectively. Susan Whitfield prepared the figures and designed and rendered Fig. 5.

References

Alroy, J., 1999. The fossil record of North American Mammals: evidence for a Palaeocene evolutionary radiation. Systematic Biology 48 (1), 107–118.

Alvarez, W., 1997. *T. rex* and the Crater of Doom. Princeton University Press, 185 pp.

Alvarez, L.W., Alvarez, W., Asaro, F., Michel, H.V., 1980. Extraterrestrial cause for the Cretaceous extinction. Science 208, 1095–1108.

Antoine, P.O., Marivaux, L., Croft, D.A., Billet, G., Ganerød, M., Jaramillo, C., Martin, T., Maëva, J., Orliac, J., Tejada, J., Altamirano, A.J., Duranthon, F., Fanjat, G., Rousse, S., Gismondi, R.S., 2012. Middle Eocene rodents from Peruvian Amazonia reveal the pattern and timing of caviomorph origins and biogeography. Proceedings of the Royal Society London B 279, 1319–1326.

Archibald, J.D., Deutshman, D.H., 2001. Quantitative analysis of the timing of origin of extant placental orders. Journal of Mammal Evolution 8, 107–124.

Archibald, D., Fastovsky, D., 2004. Dinosaur Extinction. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), The Dinosauria, second ed. University of California Press, Berkeley, pp. 672–684.

Archibald, J.D., Clemens, W.A., Padian, K., Rowe, T., Macleod, N., Barrett, P.M., Gale, A., Holroyd, P., Sues, H.-D., Arens, Horner, J.R., Wilson, G.P., Goodwin, M.B., Brochu, C.A., Lofgren, D.L., Hurlbert, S.H., Hartman, J.H., Eberth, D.A., Wignall, P.B., Currie, P.J., Weil, A., Prasad, G.V.R., Dingus, L., Courtillot, V., Milner, A., Bajpai, S., DWard, D.J., Sahni, A., 2010. Cretaceous extinctions: multiple causes. Science 328, 973.

Bleiweiss, R., 1998. Fossil gap analysis supports early Tertiary origin of trophically diverse avian orders. Geology 26, 323–326.

Boles, W.E., 1995. The world's oldest songbird. Nature 374, 1–22.

Bonde, N., 1997. A distinctive fish fauna in the basal ash-series of the Fur/Olst Formation (Upper Paleocene, Denmark). Aarhus Geosciences 6, 33–48.

Bajpai, S., Gingerich, P.D., 1998. A new Eocene achaeocete (Mammalia, Cetacea) from India and the time of origin of whales. Proceedings of the National Academy of Sciences 95, 15464–15468.

Brodkorb, P., 1963. Birds from the Upper Cretaceous of Wyoming. Proceedings of the Thirteenth International Ornithological Congress, 55–70.

Brown, J.W., Rest, J.S., Garcia-Moreno, J., Sorenson, M.D., Mindell, D.P., 2008. Strong mitochondrial DNA support for a Cretaceous origin of modern avian lineages. BMC Biology. http://dx.doi.org/10.1186/1741-7007-6-6.

Brusatte, S.L., Butler, R.J., Prieto-Márquez, A., Norell, M.A., 2012. Dinosaur morphological diversity and the end-Cretaceous extinction. Nature Communications. http://dx.doi.org/10.1038/ncomms1815.

Buffetaut, E., 2002. Giant ground birds at the Cretaceous-Tertiary boundary: extinction or survival? Geological Society of America Special Paper 356, 325–332.

Buffetaut, E., Ploeg, G. de, 2008. A large ostrich-like bird from the Late Paleocene of the Paris Region. In: Dyke, G., Naish, D., Parkes, M. (Eds.), Programme and Abstracts, SVPCA 2008. University College Dublin and the National Museum of Ireland, Dublin, Ireland, pp. 16–17.

Chao, E.C.T., Shoemaker, E.M., Madsen, B.M., 1960. First natural occurrence of coesite from Meteor Crater, Arizona. Science 132 (3421), 220–222.

Chatterjee, S., 1997. Multiple Impacts at the KT Boundary and the Death of the Dinosaurs. 30th International Geological Congress 26, 31–54.

Chatterjee, S., Guven, N., Yoshinobu, A., Donofrio, R., 2006. Shiva structure: a possible KT boundary impact crater on the western shelf of India. Museum of Texas Tech University Special Publications 50, 1–39.

Chiappe, L.M., 2007. Glorified Dinosaurs: The Origin and Evolution of Birds. John Wiley & Sons, 263 pp.

Chiappe, L.M., Dyke, J.G., 2002. The Mesozoic radiation of birds. Annual Review of Ecology and Systematics 33, 91–124.

Clarke, J.A., Tambussi, C.P., Noriega, J.I., Erickson, G.M., Ketcham, R.A., 2005. Definitive fossil evidence for the extant avian radiation in the Cretaceous. Nature 433, 305–308.

Cooper, A., Penny, D., 1997. Mass survival of birds across the Cretaceous Tertiary boundary: molecular evidence. Science 275, 1109–1113.

Cordes, A.H., 2002. A new charadriiform avian specimen from the early Maastrichtian of Cape Lamb, Vega Island, Antarctic Peninsula. Journal of Vertebrate Paleontology 22, 46A.

Cracraft, J., 1973. Continental drift, paleoclimatology, and the evolution and biogeography of birds. Journal of Zoology 169, 455–545.

Cracraft, J., 1986. The origin and early diversification of birds. Paleobiology 12, 383–469.

Cracraft, J., 2001a. Avian evolution, Gondwana biogeography and the Cretaceous-Tertiary mass extinction event. Proceedings of the Royal Society of London, Series B268, 459–469.

Cracraft, J., 2001b. Gondwana genesis. Natural History 110, 64–73.

Dawkins, R., 2004. The ancestor's tale: A pilgrimage to the dawn of life. Houghton Mifflin, Boston.

De Oliveira, F.B., Molina, E.C., Marroig, G., 2009. Paleogeography of the South Atlantic: a route for primates and rodents into the New World? In: Garber, P.A., Estrada, A., Bicca-Marques, J.C., Heymann, E., Strier, K.B. (Eds.), South American primates: comparative perspectives in the study of behavior, ecology, and conservation. Springer-Verlag, Springer, New York, pp. 55–68.

Dyke, G.J., 2001. The fossil waterfowl (Aves: Anseriformes) from the Eocene of England. American Museum Novitates No. 3354, 15 pp.

Dyke, G.J., Dortangs, R.W., Jagt, J.W., Mulder, E.W., Schulp, A.S., Chiappe, L.M., 2002. Europe's last Mesozoic bird. Naturwissenschaften 89, 408–411.

Dyke, G.J., Gulas, B.E., 2002. The fossil galliform bid *Paraortygoides* from the Lower Eocene of the United Kingdom. American Museum Novitates 3360, pp. 1–14.

Dyke, G.J., Van Tuinen, M., 2004. The evolutionary radiation of modern birds (Neornithes): reconciling molecules, morphology and the fossil record. Zoological Journal of the Linnean Society 137, 153–177.

Dyke, G.J., Nudds, R.L., Benton, M.J., 2007. Modern avian radiation across the Cretaceous-Paleogene boundary. Auk 124, 339–341.

Dyke, G.J., Lindow, B., 2009. Taphonomy and abundance of birds from the Lower Eocene. Geological Journal 44, 365–373.

Edwards, S.V., Boles, W.E., 2002. Out of Gondwana: the origin of passerine birds. Trends in Ecology and Evolution 17, 347–349.

Elzanowski, A., Stidham, T.A., 2011. A galloanserine quadrate from the Late Cretaceous of Wyoming. Auk 128, 138–145.

Ericson, P.G.P., 2000. Systematic revision, skeletal anatomy, and paleoecology of the New World early Tertiary Presbyornithidae (Aves: Anseriformes). PaleoBois 20 (2), 1–23.

Ericson, P.G.P., Parsons, T.J., Johansson, U.S., 2001. Morphological and molecular support for nonmonophyly of the Galloanserae. In: Gauthier, J., Gall, L.F. (Eds.), New Perspectives on the origin and early evolution of birds. Peabody Museum of Natural History, Yale University, New Haven, pp. 157–168.

Ericson, P.G.P., Britton, R., Elzanowski, E., Johanssons, U.S., Ilersgo, M.K., Ohlson, J.I., Parsons, T.J., Zuccon, D., Mayr, G., 2006. Diversification of Neoaves: integration of molecular sequence data and fossils. Biology Letters 2, 543–547.

Ericson, P.G.P., Klopfstein, S., Irestedt, M., Nguyen, J.M.T., Nylander, J.A.A., 2014. Dating the diversification of the major lineages of Passeriformes (Aves). BMC Evolutionary Biology 14, 8. http://dx.doi.org/10.1186/1471-2148-14-8.

Fain, M.G., Houde, P., 2004. Parallel radiations in the primary clades of birds. Evolution 58, 2558–2573.

Feduccia, A., 1995. Explosive evolution in Tertiary birds and mammals. Science 267, 637–638.

Feduccia, A., 1999. The Origin and Evolution of Birds, second ed. Yale University Press. 466 pp.

Feduccia, A., 2003. "Big bang" for Tertiary birds. Trends in Ecology and Evolution 18, 157–206.

Feduccia, A., 2012. Riddle of the Feathered Dragons: Hidden Birds of China. Yale University Press, 358 pp.

Fleming, R.F., Nichols, D.J., 1990. The fern-spore abundance anomaly at the Cretaceous-Tertiary boundary – a regional bioevent in western North America. In: Kauffman, E.G., Walliser, O.H. (Eds.), Extinction Events in Earth History, Lecture Notes in Earth Sciences, 30, pp. 347–349.

Friedman, M., 2010. Explosive morphological diversification of spiny-finned teleost fishes in the aftermath of the end-Cretaceous extinction. Proceedings of the Royal Society B 277, 1675–1683.

Friedman, M., Keck, B.P., Dornburg, A., Eytan, R.L., Martin, C.H., Darrin, C., 2013. Molecular and fossil evidence place the origin of cichlid fishes long after Gondwanan rifting. Proceedings of the Royal Society B. http://dx.doi.org/10.1098/rspb.2013.1733.

Gibbons, A., 1998. Genes put mammals in age of dinosaurs. Science 280, 675–676.

Gingerich, P.D., 2006. Environment and evolution through the Paleocene–Eocene thermal maximum. Trends in Ecology and Evolution 21, 246–253.

Grande, L., 2013. The Lost World of Fossil Lake: Snapshots from Deep Time. University of Chicago Press, 425 pp.

Graur, D., Martin, W., 2004. Reading the entrails of chickens: molecular timescales of evolution and the illusion of precision. Trends in Genetics 20, 80–86.

Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C.K., Braun, E.L., Braun, M.J., Chojnowski, J.L., Cox, W.A., Han, K.-L., Harshman, J., Huddleston, C., Marks, B.D., Miglia, K.J., Moore, W.S., Sheldon, F.H., Steadman, D.W., Witt, C.C., Yuri, T., 2008. A phylogenomic study of birds reveals their evolutionary history. Science 320, 1763–1768.

Haddrath, O., Baker, A.J., 2012. Multiple nuclear genes and retroposons support vicariance and dispersal of the palaeognaths, and an Early Cretaceous origin of modern birds. Proceedings of the Royal Society B. http://dx.doi.org/10.1098/repb.2012.1630.

Hansford, D., 2008. Dino-era seabird fossils found in New Zealand. National Geographic News. http://news.nationalgeographic.com/news/2008/02/080222-seabird-fossils.html (accessed 02.09.08).

Harshman, J., Braun, E.L., Braun, M.J., Huddleston, D.J., Bowie, R.C.K., Chonjnowski, J.L., Hackett, S.J., Han, K.-L., Kimball, R.T., Marks, K.J., Miglia, W., Moore, S., Teddy, S., Sheldon, F.H., Steadman, D.W., Steppan, S.J., Witt, C.C., Yuri, T., 2008. Phylogenomic evidence for multiple losses of flight in ratite birds. Proceedings of the National Academy of Sciences 105 (36), 13462–13467.

Haussler, D., 2009. Genome 10K: a proposal to obtain whole-genome sequence for 10,000 vertebrates. Journal of Heredity 100, 63–72.

Hayden, E.C., 2009. 10,000 genomes to come: vertebrates in line for massive sequences project. Nature 462, 21.

Hedges, S.B., Parker, P.H., Sibley, C.G., Kumar, S., 1996. Continental breakup and the ordinal diversification of birds and mammals. Nature 381, 226–229.

Hicks, J.F., Johnson, J.R., Obradovich, J.D., Tauxe, L., Clark, D., 2002. Magnetostratigraphy and geochronology of the Hell Creek and basal Fort Union Formations of southwestern North Dakota and a recalibration of the age of the Cretaceous-Tertiary boundary. Geological Society of America Special Paper 361, 35–56.

Hope, S., 2002. The Mesozoic radiation of Neornithes. In: Chiappe, L.M., Witmer, L.M. (Eds.), Mesozoic Birds: Above the Heads of Dinosaurs. University of California Press, pp. 339–388.

Houde, P., 1988. Palaeognathous birds from the early Tertiary of North America. Publications of the Nuttall Ornithological Club 22, 1–148.

Houde, P., Olson, S.L., 1981. Palaeognathous carinate birds from the early Tertiary of North America. Science 214, 1236–1237.

Jardine, P., 2011. The Paleocene-Eocene Thermal Maximum. Palaeontology Online Volume 1. Article 5, 1–7.

Jablonski, D., 1994. Extinctions in the fossil record (and discussion). Philosophical Transactions of the Royal Society of London, Series B 344, 11–17.

James, H.F., 2005. Overview: Paleogene fossils and the radiation of modern birds. Auk 122 (4), 1049–1054.

Janzen, D.H., 1995. Who survived the Cretaceous? Science 268, 785.

Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K., Mooers, A.K., 2012. The global diversity of birds in space and time. Nature 491, 444–448.

Kaiser, G., Dyke, G., 2011. Introduction: changing the questions in avian paleontology. In: Dyke, G., Kaiser, G. (Eds.), Living Dinosaurs: The Evolutionary History of Modern Birds. John Wiley & Sons, pp. 3–7.

Kawaragi, K., Sekine, Y., Kadono, T., Sugita, S., Ohno, S., Ishibashi, K., Kurosawa, K., Matsui, T., Ikeda, S., 2009. Direct measurements of chemical composition of shock induced gases from calcite: an intense global warming after the Chicxulub impact due to the indirect greenhouse effect of carbon monoxide. Earth and Planetary Science Letters 282, 56–64.

Keller, G., Adatte, T., Gardin, S., Bartolini, A., Bajpai, S., 2008. Main Deccan volcanism phase ends near the K–T boundary: Evidence from the Krishna-Godavari Basin, SE India. Earth and Planetary Science Letters 268 (3–4), 293–311.

Keller, G., Abramovich, S., Berner, Z., Adatte, T., 2009. Biotic effects of the Chicxulub impact, K-T catastrophe and sea level change in Texas. Palaeogeography, Palaeoclimatology, Palaeoecology 271, 52–68.

Koutsoukos, E.A.M., 2005. The K-T boundary. In: Koutsoukos (Ed.), Applied Stratigraphy, Chapter 7. Springer-Verlag, pp. 147–161.

Kring, D.A., 2007. The Chicxulub impact event and its environmental consequences at the Cretaceous-Tertiary boundary. Palaeogeography, Palaeoclimatology, Palaeoecology 255, 4–21.

Kring, D.A., Durda, D., 2002. Trajectories and the distribution of material ejected from the Chicxulub impact crater: implications for post-impact wildfires. Journal of Geophysical Research 107. http://dx.doi.org/10.1029/2001JE001523.

Kring, D.A., Durda, D.D., Dec. 2003. The day the world burned. Scientific American, 98–105.

Kumar, S., Hedges, S.B., 1998. A molecular timescale for vertebrate evolution. Nature 392, 917–920.

Kurochkin, E.N., 2005. The assemblage of Cretaceous birds in Asia. In: Ailiing, S., Wang, Y. (Eds.), Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers, Paleontological Institute Special Issue. China Ocean Press, Beijing, pp. 203–208.

Kurochkin, E.N., Dyke, G.J., Karhu, A.A., 2002. A new presbyornithid (Aves, Anseriformes) from the Late Cretaceous. American Museum Novitates 3386, pp. 1–11.

Labandeira, C.C., Johnson, K.R., Wilf, W., 2002. Impact of the terminal Cretaceous event on plant–insect associations. Proceedings of the National Academy of Sciences of the United States of America 99 (4), 2061–2066.

Lindow, B.E.K., 2011. Bird evolution across the K-Pg boundary and the basal neornithine diversification. In: Dyke, G., Kaiser, G. (Eds.), The Evolutionary History of Modern Birds. John Wiley & Sons, pp. 338–354.

Lindow, B.E.K., Dyke, G.J., 2006. Bird evolution in the Eocene: climate change in Europe and a Danish fossil fauna. Biological Reviews 81, 483–499.

Longrich, N.R., 2009. An ornithurine-dominated avifauna from the Belly River Group (Campanian, Upper Cretaceous) of Alberta, Canada. Cretaceous Research 30, 161–177.

Longrich, N.R., Tokaryk, T.T., Field, D., 2011. Mass extinction of birds at the Cretaceous-Paleogene (K–Pg) boundary. Proceedings of the National Academy of Sciences 108 (37), 15253–15257.

Longrich, N.R., Bhullar, A.-B.S., Gauthier, J.A., 2012. Mass extinction of lizards and snakes at the Cretaceous-Paleogene boundary. Proceedings of the National Academy of Sciences 109 (52), 21396–21401.

Lyson, T.R., Bercovici, A., Chester, S.G.B., Sargis, E.J., Pearson, D., Joyce, W.G., 2011. Dinosaur extinction: closing the '3 m gap'. Biology Letters 7, 925–928.

MacLeod, N., Rawson, P.F., Forey, P.L., Boudagher-Fadel, M.K., Brown, P.R., Burnett, J.A., Chambers, P., Culver, S., Evans, S.E., Jeffery, C., Kaminski, M.A., Lord, A.R., Milner, A.C., Milner, A.R., Morris, N., Owen, E., Rosen, B.R., Smith, A.B., Taylor, P.D., Urquhart, E., Young, J.R., 1997. The Cretaceous-Tertiary biotic transition. Journal of the Geological Society 154 (2), 265–292.

Marsh, O.C., 1892. Notes on Mesozoic vertebrate fossils. American Journal of Science, Series 3 (55), 171–175.

Matsui, T., Imamura, F., Tajika, E., Nakano, Y., Fujisawa, Y., 2002. Generation and propagation of a tsunami from the Cretaceous-Tertiary impact event. In: Koeberl, C., MacLeod, K.G. (Eds.), Catastrophic Events and Mass Extinctions: Impacts and Beyond. Geological Society of America Special Paper 356, Boulder, Colorado, pp. 69–77.

Mayr, G., 2004. A partial skeleton of a new fossil loon (Aves, Gaviiformes) from the early Oligocene of Germany with preserved stomach content. Journal of Ornithology 145, 281–286.

Marshall, C.R., 1997. Confidence intervals on stratigraphic ranges with nonrandom distribution of fossil horizons. Paleobiology 23, 165–173.

Martin, L.D., Kurochkin, E.N., Tokaryk, T.T., 2012. A new evolutionary lineage of diving birds from the Late Cretaceous of North America and Asia. Palaeoworld 21, 59–63.

Mayr, G., 2005. The Paleogene fossil record of birds in Europe. Biological Reviews 80, 515–542.

Mayr, G., 2007. The birds from the Paleocene fissure filling of Walbeck (Germany). Journal of Vertebrate Paleontology 27 (2), 394–408.

Mayr, G., 2009. Paleogene Fossil Birds. Springer-Verlag, Berlin, 262 pp.

Mayr, G., 2013. Perspective: The age of the crown group of passerine birds and its evolutionary significance – molecular calibrations versus the fossil record. Systematics and Biodiversity 11 (1), 7–13.

Mayr, G., Leonid, G., Zvonok, E., 2013. The tarsometatarsus of the Middle Eocene loon *Colymbiculus udovichenkoi*. 2013. In: Göhlich, U.B., Korh, A. (Eds.), Paleornithological Research 2013 – Proceedings of the 8th International Meeting of the Society of Avian Paleontology and Evolution, Vienna. Natural History Museum, Vienna, pp. 17–22.

Melchor, R.N., De Valais, S., Genise, J.F., 2013. A Late Eocene date for Late Triassic bird tracks. Nature 417, 936–938.

Meredith, R.W., Janečka, J.E., Gatesy, J., Ryder, O.A., Fisher, C.A., Teeling, E.C., Goodbla, A., Eizirik, E., Simão, T.L., Stadler, T., Rabosky, D.L., Honneycutt, R.L., Flynn, J.J., Ingram, C.M., Steiner, C., Williams, T.L., Robinson, T.J., Burk-Herrick, A., Westerman, M., Ayoub, N.A., Springer, M.S., Murphy, W.J., 2011. Impacts of the Cretaceous terrestrial revolution and KPg extinction on mammal diversification. Science 334, 521–524.

Monmaney, T., 1993. The dinosaur heretic. The New Yorker May 31, 42–52.

Mourer-Chauviré, C., Senut, B., Pci, M., 1996. Le plus ancien représentant du genre *Struthio* (Aves, Struthionidae), *Struthio coppesi* n. sp. du miocéne intérieur du Namibie. Acad. Des. Sci., Compte Rendu, ser 2A 332, 325–332.

Mourer-Chauviré, C., Tabuce, R., Essid, E.M., Marivaux, L., Khayati, H., Vianey-Liaud, M., Ali, M.B.H., 2013. A new taxon of stem group Galliformes and the earliest record for stem group Cuculidae from the Eocene of Djebel Chambi, Tunisia. In: Göhlich, U.B., Korh, A. (Eds.), Paleornithological Research 2013 – Proceedings of the 8th International Meeting of the Society of Avian Paleontology and Evolution, Vienna. Natural History Museum, Vienna, pp. 1–15.

Murphy, W.J., Eizirik, E., Johnson, W.E., Zhang, Y.P., Ryder, O.A., O'Brien, S.J., 2001. Molecular phylogenetics and the origins of placental mammals. Nature 409, 614–618.

Mullen, L., 2004. Shiva: Another K–T impact? Astrobiology Magazine, 2012-03-29.

Near, T.J., Eytan, R.I., Dornburg, A., Kuhn, K.L., Moore, J.A., Davis, M.P., Wainwright, P.S., Friedman, M., Smith, W.L., 2012. Resolution of ray-finned fish phylogeny and timing of diversification. Proceedings of the National Academy of Sciences 106, 13410–13414.

Nichols, S.J., Johnson, K.R., 2008. Plants and the K-T Boundary. Cambridge University Press, 280 pp.

Noriega, J.I., Tambusi, C.P., 1995. A Late Cretaceous Presbyornithidae (Aves: Anseriformes) from Vega Island, Antarctic Peninsula: paleobiogeographical implications. Ameghiniana 32, 57–61.

Novacek, M.J., 1999. 100 million years of land vertebrate evolution: the Cretaceous-early Tertiary transition. Annals of the Missouri Botanical Garden 86, 230–258.

O'Donoghue, J., 2010. Flight of the living dead. New Scientist 208 (2790), 36–40.

Oldfield, R.G., 2004. Saltwater cichlids. Knowledge of salinity and preference may allow new species combinations and improved husbandry in aquaria. Freshwater and Marine Aquarium 27 (8), 98–104.

O'Leary, M.A., Bloch, J.I., Gaudin, T.J., Flynn, J.J., Giallombardo, A., Giannini, N.P., Goldberg, S.L., Kraatz, B.P., Lou, Z.-X., Meng, J., Ni., X., Novacek, M.J., Perini, R.A., Raqndall, Z.S., Rougier, G.W., Sargis, E.J., Silcox, M.T., Simmons, N.B., Spaulding, M., Velazdo, P.M., Weksler, M., Wible, J.R., Cirranello, A.L., 2013. The placental mammal ancestor and the post-K-Pg radiation of placentals. Science 339, 662–667.

Olson, S.L., 1973. Evolution of the rails of the South Atlantic (Aves: Rallidae). Smithsonian Contributions to Zoology 152, 1–53.

Olson, S.L., 1977. A Lower Eocene frigatebird from the Green River Formation of Wyoming (Aves: Neornithes). Smithsonian Contributions to Paleobiology 89, 1–33.

Olson, S.L., Feduccia, A., 1980. *Presbyornis* and the origin of the Anseriformes (Aves: Charadriomorphae). Smithsonian Contributions to Zoology 323, 1–24.

Olson, S.L., James, H.F., 1991. Description of thirty-two species of birds from the Hawaiian Islands. Part I. Non-Passeriformes. Ornithological Monographs 45, 1–88.

Olson, S.L., Parris, D.C., 1987. The Cretaceous birds of New Jersey. Smithsonian Contributions to Paleobiology 63, 1–22.

Pacheco, A., Battistuzzi, F.U., Lentino, M., Aguilar, R.F., Kumar, S., Escalante, A.A., 2011. Evolution of modern birds revealed by mitogenomics: timing the radiation and origin of modern orders. Molecular Biology and Evolution 26 (8), 1927–1942.

Paton, T., Haddrath, O., Baker, A.J., 2002. Complete mitochondrial sequences show that modern birds are not descended from transitional shorebirds. Proceedings of the Royal Society of London series B 269, 839–846.

Pennisi, E., 2008. Building the tree of life, genome by genome. Science 320, 1716–1717.

Peters, D.S., 1987. *Juncitarsus merkeli* n. sp. Stütz die Ableitung der Flamingos von Regenpfeifervögeln (Aves: Charadriiformes: Phoenicopteridae). Courier Forschungsinstitut Senckenberg 97, 141–155.

Poe, S., Chubb, A.L., 2004. Birds in a bush: five genes indicate explosive evolution of avian orders. Evolution 58, 404–415.

Poux, C., Chevert, P., Huchon, D., de Jong, W.W., Douzery, E.J.P., 2006. Arrival and diversification of caviomorph rodents and platyrrhine primates in South America. Systematic Biology 55, 228–244.

Prager, E.M., Wilson, A.C., 1980. Phylogenetic relationships and rates of evolution in birds. Proceedings of the Seventeenth International Ornithological Congress, 1209–1214.

Pratt, R.C., Gibb, G.C., Morgan-Richards, M., Phillips, M.J., Hendy, M.D., Penny, D., 2008. Toward resolving deep Neoaves phylogeny: signal enhancement, and priors. Molecular Biology and Evolution 26 (2), 313–326.

Pulquerio, M.J.F., Nichols, R.A., 2006. Dates from the molecular clock: how wrong can we be? Trends in Ecology and Evolution 22 (4), 180–184.

Reguero, M.A., Tambussi, C.P., Coria, R.A., Marenssi, S.A., 2013. Late Cretaceous from the James Ross Basin West Antarctica. Geological Society, London, Special Publications. http://dx.doi.org/10.1144/SP381.20.

Rehan, S.H., Leys, R., Schwarz, M.P., 2013. First evidence for a massive extinction event affecting bees close to the K-T boundary. PLoS ONE 8 (10), e76683. http://dx.doi.org/10.1371/journal.pone.0076683.

Robertson, D.S., McKenna, M.C., Toon, O.B., Hope, S., Lillegraven, A.J., 2004. Survival in the first hours of the Cenozoic. Geological Society of America Bulletin 116, 760–776.

Rose, K.D., 2006. The Beginning of the Age of Mammals. Johns Hopkins University Press, 488 pp.

Schluter, D., 2000. The ecology of adaptive radiation. Oxford University Press, Oxford.

Schulte, P., Alegret, L., Arenillas, I., Arz, J.A., Barton, P.J., Brown, P.R., Bralower, T.J., Christeson, G.L., Claeys, P., Cockell, C.S., Collins, G.S., Deutsch, A., Goldin, T.J., Goto, K., Grajales-Nishimura, J.M., Grieve, R.A.F., Gulick, S.P.S., Johnson, K.R., Kiessling, W., Koeberl, C., Kring, D.A., MacLeod, J.G., Matsui, T., Melosh, J., Montanari, A., Morgan, J.V., Neal, C.R., Nichols, D.J., Norris, R.D., Pierazzo, E., Ravizza, G., Recolledo-Vieyra, M., Reimold, W.U., Robin, E., Salge, T., Speijer, R.P., Sweet, A.R., Urrutia-Fucugauchi, J., Vajda, V., Whalen, M.T., Willumsen, P.S., 2010. The Chicxulub asteroid impact and mass extinction at the Cretaceous-Paleogene boundary. Science 327, 1214–1218.

Steadman, D.W., 2006. Extinction and Biogeography of Tropical Pacific Birds. University of Chicago Press, Chicago.

Stidham, T.A., 1998. A lower jaw from a Cretaceous parrot. Nature 396, 29–30.

Stresemann, E., 1959. The status of avian systematics and its unsolved problems. Auk 76, 269–280.

Tokaryk, T.T., Cumbaa, S.L., Storer, J.E., 1997. Early diverse Late Cretaceous birds from Saskatchewan Canada: oldest diverse avifauna known from North America. Journal of Vertebrate Paleontology 17, 172–176.

Tschudy, R.H., Tschudy, B.D., 1986. Extinction and survival of plant life following the Cretaceous-Tertiary boundary event, western interior, North America. Geology 14, 667–670.

Thewissen, J.G.M., Bajpai, S., 2001. Whale origins as a poster child for macroevolution. Bioscience 51, 1037–1049.

Vajda, V., Raine, J.I., Hollis, C.J., 2001. Indication of Global Deforestation at the Cretaceous–Tertiary Boundary by New Zealand Fern Spike. Science 294, 1700–1702.

Vajda, V., McLoughlin, S., 2004. Fungal Proliferation at the Cretaceous–Tertiary Boundary. Science 303, 1489–1490.

Van Tuinen, M., Stidham, T.A., Hadly, E.A., 2006. Tempo and mode of modern bird evolution observed with large-scale taxonomic sampling. Historical Biology 18, 205–221.

Ward, J.A., Wymann, R.L., 1977. Ethology and ecology of cichlid fishes of the genus *Etroplus* in Sri Lanka: preliminary findings. Environmental Biology of Fishes 2, 137–145.

Whitfield, A.K., Blaber, S.J.M., 1979. The distribution of the freshwater cichlid *Sarotherodon mossambicus* in estuarine ecosystems. Environmental Biology of Fishes 4, 77–81.

Wible, J.R., Rogier, G.W., Novacek, M.J., Asher, R.T., 2007. Cretaceous eutherians and Laurasian origin for placental mammals near the K/T boundary. Nature 447, 1003–1006.

Wilf, P., Johnson, K.R., 2004. Land plant extinction at the end of the Cretaceous: a quantitative analysis of the North Dakota megafloral record. Paleobiology 30 (3), 347–368.

Wilf, P., Labandeira, C.C., Johnson, K.R., Ellis, B., 2006. Decoupled Plant and Insect Diversity After the End-Cretaceous Extinction. Science 313 (5790), 1112–1115.

Wyles, J.S., Kunkel, J.G., Wilson, A.C., 1983. Birds, behavior, and anatomical evolution. Proceedings of the National Academy of Sciences 80, 4394–4397.

Yoder, A.D., 2013. Fossils versus clocks. Science 339, 656–657.