Chapter 15
Crossing the Boundary

The early history of birds is hotly debated because it offers a new perspective on both the K-T extinction and one of the greatest *adaptive radiations* in vertebrate history. Adaptive radiation is evolutionary diversification on a grand scale, often occurring in a relatively short geological time span. Lineages split again and again, rapidly filling environmental niches with a new dynasty of novel species.

Tropical forests and islands have hosted some of the greatest rapid adaptive radiations in history. Organisms that somehow invade an island at the right time or find an unoccupied level of forest canopy may exploit a wide new landscape of opportunities for themselves and their offspring. The famous adaptive radiation of finches and tortoises on the Galápagos Islands profoundly shaped Darwin's ideas on evolution and natural selection. Archipelagos, lakes, caves, and rift valleys may all serve as spawning grounds for adaptive radiations by providing isolation from parent populations and new ecological opportunities for the proliferating species. The impact of an adaptive radiation upon the local economy of nature can be far-reaching.

Non-avian dinosaurs underwent an adaptive radiation during the Mesozoic that generated the hundreds of species and enormous diversity of shapes described earlier[1]. But that was just the beginning. The adaptive radiation of avian dinosaurs was even greater, yielding more than 9,000 living species and thousands more that arose and became extinct over the course of their Tertiary history. Because birds occupy most of the paths on the dinosaurian map, paleontologists have begun to ask, how was diversity of the *entire* dinosaurian lineage affected at the end of the Cretaceous? When did the great adaptive radiation of birds begin, and what environmental factors may have triggered it?

Alan Feduccia (University of North Carolina) and his associates contend that birds underwent a Mesozoic proliferation before being nearly wiped out at the end of the Cretaceous[2]. Only a single lineage crossed the K-T boundary, but this was followed by an explosive adaptive radiation of birds in the 5 million to 10 million years following the great extinction. Like the Phoenix, modern birds rose from the ashes, reborn from a lone Tertiary survivor (fig. 15.01). According to this hypothesis, that post-extinction explosive radiation over the last 65 million years generated the 9,000 species alive today. Feduccia argues that birds and mammals both experienced parallel, contemporaneous episodes of Mesozoic diversification and extinction, before radiating explosively in the Tertiary. An extraterrestrial event like an asteroid impact probably shaped the common course of evolution for both. These biologists rejects the idea that birds are the descendants of Mesozoic dinosaurs. Instead, they argue that the hierarchy of similarities outlined in the preceding chapters represents convergent evolution, and that the roots of avian evolution remain shrouded in mystery. Once again, we cross paths with scientists using the theory of homoplasy to explain the resemblance between birds and dinosaurs.

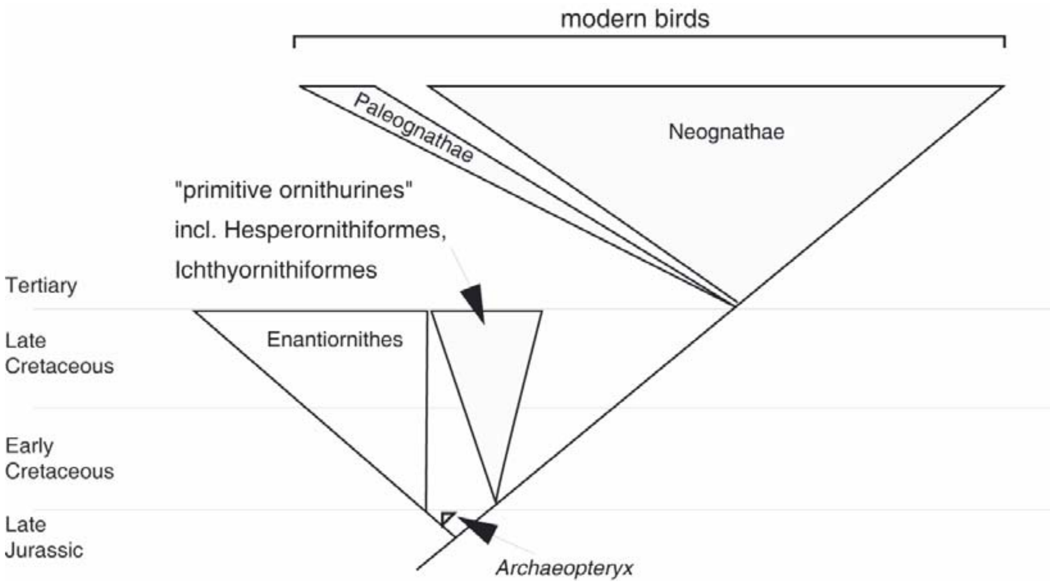

Figure 15.01 Alan Feduccia's controversial hypothesis about the history of avian diversity depicts an episode of Mesozoic diversification that was nearly chopped off at the K-T boundary. The catastrophic extinction was followed by an "explosive" Tertiary radiation of modern birds from a small group of survivors.

The opposing view actually represents a much older idea recast in a modern phylogenetic mold. It points to the beginning for modern avian diversity on the map of theropod dinosaurs in the Early or mid-Cretaceous. Although there were losses at the end of the Cretaceous, birds flew across the K-T boundary relatively unscathed. The modern architects of this view are Joel Cracraft and Luis Chiappe, of the American Museum of Natural History. Cracraft was a pioneer in using cladistic methods for phylogenetic analysis, which he applied to mapping the early history of birds[3]. Chiappe, who has handled nearly all of the known Mesozoic bird specimens, is extending Cracraft's map to include new discoveries of fossil birds[4]. By plotting Mesozoic birds on the evolutionary map with the help of computers, these and other scientists[5] point to evidence for an ancient diversification of modern birds. Although birds suffered some Late Cretaceous losses, the common ancestor of living species is twice as old as suggested by Feduccia's Phoenix hypothesis. If this hypothesis is true, avian history was shaped by much slower, terrestrial processes.

Did birds rebound from a catastrophic near miss with extinction? Did the history of birds parallel that of mammals in an explosion of Tertiary diversification? Both of these hypotheses are predictive and can be tested to some extent. To see how this is done, it is helpful first to examine how biologists map diversity through time and deal with the incompleteness of the fossil record.

Discovering Ghosts

One of the grandest pre-Darwinian portrayals of the history of Life's diversity is the division of the geologic timescale into three successive Ages. First came the *Age of Fishes* (Paleozoic), followed by the *Age of Reptiles* (Mesozoic), and then the *Age of Mammals* (Cenozoic = Tertiary + Quaternary). When these names were coined, there were no tetrapod fossils known from Paleozoic rocks, so the *Age of Fishes* seemed a fitting title. Reptiles first appeared in younger Mesozoic rocks. Mesozoic bird and mammal fossils were unknown, so the *Age of Reptiles*, which became *The Age of Dinosaurs* in Richard Owen's hands, was another appropriate title. The *Age of Mammals* was named because giant reptiles were absent and instead mammals were abundantly preserved through out the Cenozoic fossil record.

The discovery of Mesozoic mammals, which did not belong in the Age of Reptiles, was a shock to the 19th century scientific community. A few years later, the discovery of *Archaeopteryx* produced the same shock all over again. As the fossil record grew, more fossils violated the boundaries between Ages. The scientists most surprised by these discoveries were those who accepted the sequence of fossils as representing successive episodes of divine creation or biblical floods. But evolutionists had predicted the discovery of 'missing links' between all the paths on the map of Life. They argued that the known fossil record for any lineage is only a small sample of its complete history. Hidden paths of relationship extend deeper into the past to connect all fossil and modern species on a single map of genealogy. Since the discovery of *Archaeopteryx*, this inference has been tested and confirmed by countless fossil discoveries.

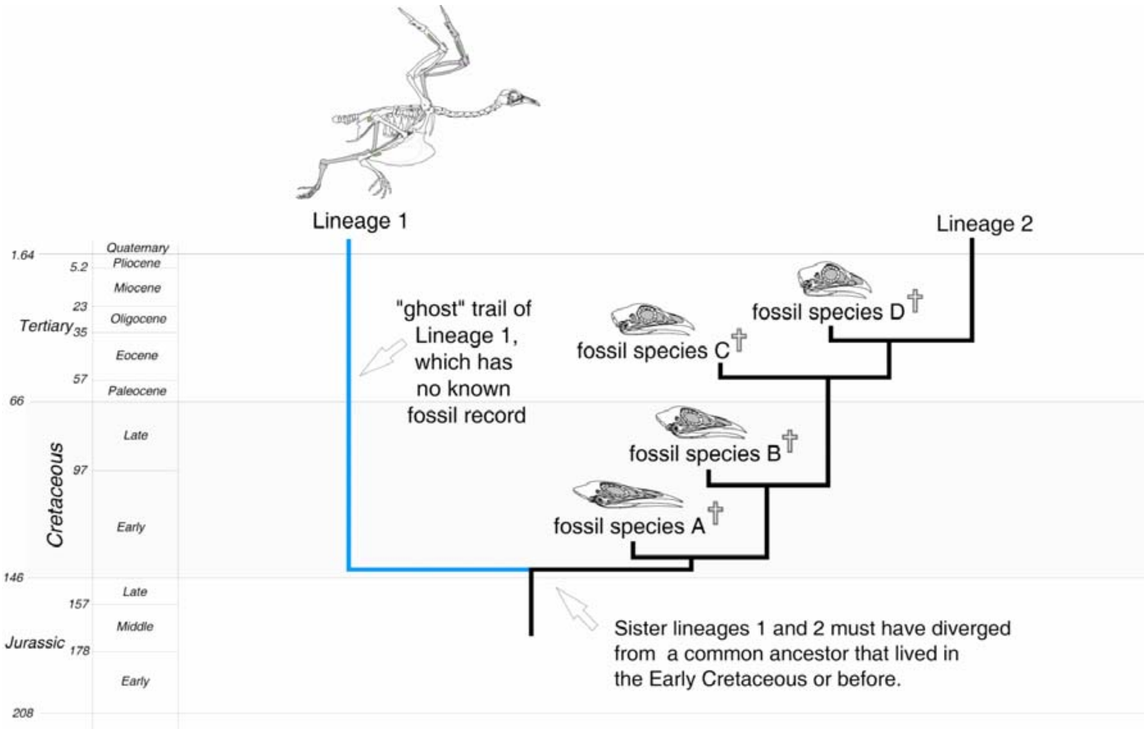

Figure 15.02 If this map is correct, that living lineages 1 and 2 are sisters, then both must have been present in the Cretaceous, and both must have survived across the K-T boundary. Although we have found no fossils for lineage 1 and have no idea of just how diversified it was in the past, we can connect its history in time to lineage 1, which did leave a fossil record. Crosses denote extinct species.

Emerging from modern phylogenetic mapping is an even more vivid appreciation for these 'hidden' lineages than the 19th century evolutionists had. One fossil, accurately plotted on the phylogenetic map, can potentially provide new evidence on the time of origin for several lineages. Imagine two sister lineages, originating from an ancestral species that lived during the Cretaceous, and both represented by living species. One lineage leaves fossils from the Cretaceous onward, while the sister lineage leaves no fossils at all. Because they are sister lineages (a hypothesis subject to independent phylogenetic testing), then both must have been present together from the Cretaceous onward. Although only one line is documented directly by Mesozoic fossils, the map indicates that both lineages successfully crossed the K-T boundary.

The sister lineage that left no Mesozoic fossils is sometimes referred to as a *ghost lineage*, based on the work of Mark Norell at the American Museum of Natural History[6]. Although ghost lineages cannot be seen directly in the fossil record, they exist on the phylogenetic map (fig. 15.02). One of the great strengths of any mapping enterprise is the capacity it generates to extrapolate between known species. Once plotted on the map, the ghost-like lines of inferred relationship can be identified and counted, revealing the diversity within tetrapods that was not captured by the preservation or discovery of fossils. Ghost lineages predict what the fossil record should eventually yield, so they can be tested through both field work and further phylogenetic analysis.

The two competing hypotheses of avian diversification can be tested by the phylogenetic map for Cretaceous and living birds. Likewise, the claim that birds and mammals shared parallel histories, can be examined by comparing phylogenies for both lineages. So, with ghost lineages in mind, let's now examine the histories of mammals and birds.

Mesozoic Mammals

Richard Owen played a major role in validating the first discoveries of Mesozoic mammals[7]. Two tiny jaws of Jurassic mammals were discovered in the Stonesfield Slate of Britain, in 1812. Georges Cuvier identified them as Mesozoic mammals, linking them to living marsupials like the opossum. But many other contemporary naturalists rejected as impossible the idea that mammals lived in the Age of Reptiles. Yet, several more specimens were unearthed over the next few years. These fossils were surprising to Owen, but after personally inspecting them and comparing them to modern mammals, Owen convinced the scientific community that mammals were indeed present in England during the Age of Reptiles. Since then, many more Mesozoic mammal have been discovered. Scientists now universally accept that mammals were not only present in the Mesozoic, but that they had achieved a global distribution long before the era ended[8].

Mesozoic mammals were uniformly small (fig. 15.03). Most were the size of modern mice and shrews, so their bones were poorly constructed for preservation in the fossil record. But their tiny teeth are much more durable. The mammalian dentition evolved to unparalleled levels of complexity and diversity during the Mesozoic. Teeth are very hard and last long after the rest of the skeleton is destroyed by natural processes. They can even pass through the intestinal tract of a predator and remain identifiable. So, mammalian teeth are often fossilized, but their very small size makes them difficult to find. About 30 years ago, a technique known as screen washing was developed to promote the recovery of tiny fossil teeth. Large volumes of sediments are sieved, producing a concentrate rich in tooth-sized particles. The concentrate is then sorted under a microscope to pick out the teeth and other fossils. Although tedious and labor-intensive, screen washing has enabled paleontologists to successfully recover teeth from dozens of Mesozoic mammal species that have now been named.

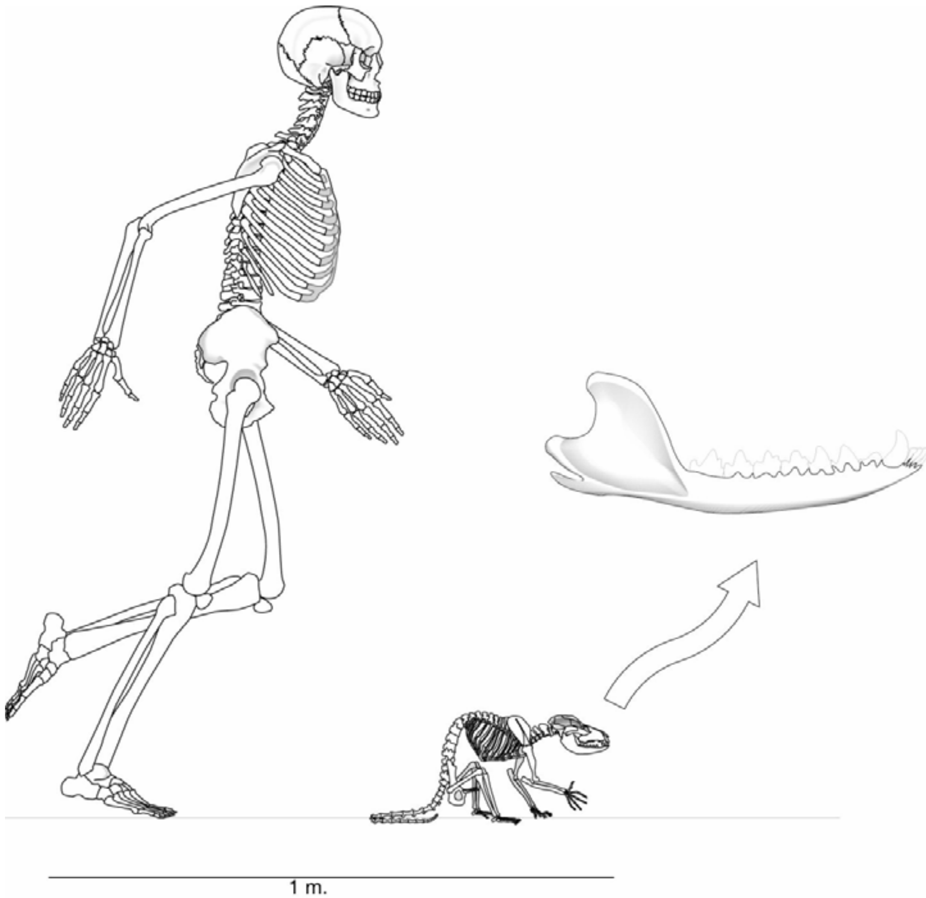

Figure 15.03 Mesozoic mammals were rarely larger than the modern opossum, and they left little to the fossil record besides isolated jaws and teeth, the hardest parts of the skeleton.

Some unbelievably rich fossil sites in several parts of the world provided complete jaws, skulls, and skeletons of Cretaceous mammals. These have been especially important for phylogenetic mapping. When only teeth were known, it was difficult to precisely map the relationships among Mesozoic mammals. A recent discovery from Greenland by Farish Jenkins (Harvard University) and associates highlighted the problem[9]. Individual teeth of an extinct lineage named Haramiyidae had long been known from Late Triassic and Early Jurassic deposits in many parts of the world. After many years of speculating on what harimiyids looked like and who they were related to, Jenkins discovered a complete skull. The upper and lower teeth of the animal had been mistakenly identified as separate species, based on isolated teeth collected by earlier paleontologists. One species was named for upper teeth while the other was named for lowers. The skull showed that the two “species” were parts of the same animal. Complete specimens provide a much stronger basis for phylogenetic analysis than teeth alone.

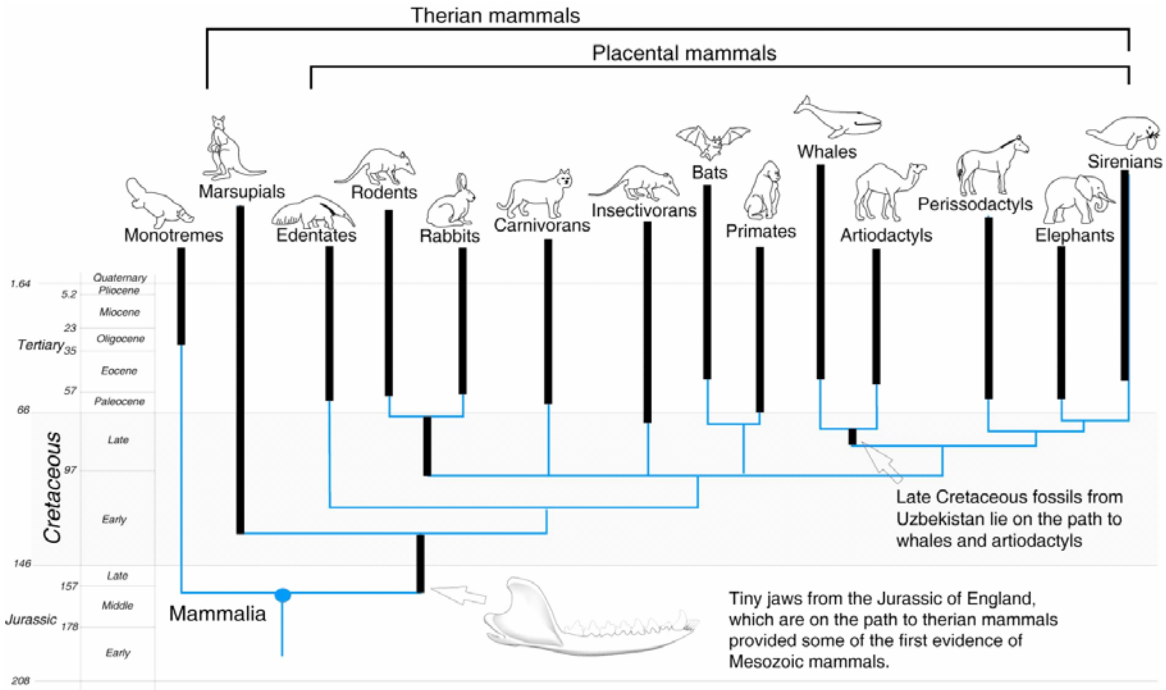

Figure 15.04 The solid black lines indicate the range of each lineage, based on known fossils. The blue lines are ghost lineages that represent the approximate duration in time for each lineage, based on what we know about their relationships (based on Archibald, J. D. 1996b. Fossil evidence for a Late Cretaceous origin of "hoofed" mammals. Science 272:1150-1153.)

It has long been clear that the Age of Mammals started well before the Age of Dinosaurs ended. But the true diversity of Mesozoic mammals is only now becoming clear as the Mesozoic fossils are plotted on phylogenetic maps. One important assemblage of fossil mammals, dating back about 85 million years, was collected over the last two decades by the late Russian paleontologist Lev Nessov[10]. Without the assistance of a field vehicle, Nessov hitch-hiked and walked vast distances while prospecting for fossils in remote regions of the Kyzylkum Desert south of the Aral Sea. He usually collected only what he could carry out with him. As a result, Nessov is one of the few paleontologists who praised Mesozoic mammals for their small size! Although he couldn't collect the dinosaur skeletons he found, he brought a great diversity of beautifully preserved Cretaceous mammals to Saint Petersburg.

Nessov's American colleague David Archibald, who we met in Part I, was the first to plot these on an evolutionary map of mammals[11]. Some fossils preserve characteristics found only within the *ungulate* lineage. Today, ungulates are highly diversified and include horses, rhinos, tapirs, pigs, deer, elephants, hyraxes, whales, sea cows, and aardvarks. Archibald's phylogenetic analysis placed some of the Kyzylkum fossils at the base of the ungulate line (fig. 15.04). Before Nessov's discoveries, ungulates were known only from Cenozoic rocks of North America. Most paleontologists thought that ungulates originated in North America and later spread to Asia. But now our map indicates that the origin and early diversification of ungulates began in Asia during the Cretaceous, where they crossed the K-T boundary. Ungulates later spread to North America via land bridges at the Bering Strait, and by island hopping across the North Atlantic, which was much narrower than it is today.

In mapping Nessov's fossils as Cretaceous ungulates, Archibald drew ghost lineages for many other mammalian groups into the Cretaceous, extending their suspected ranges 20 million years further into the past (fig. 15.04). Based on current maps, the lineages including modern sloths, rabbits, rodents, tree shrews, bats, and carnivores had all originated and begun to diverge by the end of the Cretaceous. It now looks as though even our own primate lineage originated in the Cretaceous and survived the K-T boundary. We haven't found their fossils yet, but the map predicts that with time and sweat paleontologists may eventually do so. Mapping both fossils and ghost lineages against time contradicts Feduccia's argument - modern mammalian diversity is rooted deeply in the Age of Dinosaurs.

Mapping Cretaceous Bird Diversity

The Mesozoic fossil record of birds reflects the same problems, only worse. Globally, there are only a few dozen named species of Mesozoic birds. Precise estimates are difficult estimate owing to the fragmentary nature and uncertain identifications of a large percentage of specimens. Shorebirds and waterbirds have the best fossil records, because they live close to potential burial sites. Terrestrial birds must withstand more abrasive transport by streams and rivers. The rarity of terrestrial bird fossils is a global problem that can be appreciated best on a local scale. For example, over the last three decades, about 150,000 vertebrate fossils have been collected from rocks spanning the K-T boundary in Alberta and Montana by Berkeley's Museum of Paleontology. Only about 30 are birds, representing five different species[12]. Even more than mammals, knowledge of Mesozoic birds has been hard-won despite decades of searching. Only now are we beginning to see the acceleration of Mesozoic bird discoveries that began with mammals three decades ago.

Another problem is that important regions of bird phylogeny remain unmapped. This is ironic because birds have been a favorite subjects of naturalists for centuries. A vast scientific literature of observations exists about breeding behavior, songs, nesting, migratory pathways, physiology, diet, embryology, and genetics. Many of the smaller roads on the map of avian phylogeny are now charted in some detail, but the connections between some of the major avian highways are highly controversial. So, it is hard to determine what unique and diagnostic features were present in the ancestors of many large modern groups. What would the ancestral chicken or duck look like if you discovered it? Today, no one has trouble distinguishing between ducks and chickens, but we have yet to sort out exactly what the basal members of these groups looked like or to unequivocally recognize their oldest fossil relatives.

With these caveats in mind, what can we say about how birds fared during the K-T transition? The best-known Cretaceous bird fossils belong to Hesperornithiformes, Ichthyornithiformes, and Enantiornithes, which we met in the previous chapter. These and several others became extinct at or before the end of the Cretaceous. However, other Cretaceous fossils found around the world do not belong to any of these lineages, and they document an unsuspected diversity of Late Cretaceous birds. Some have been placed on the evolutionary pathways to living bird lineages, and they offer direct clues about avian survivorship across the K-T boundary.

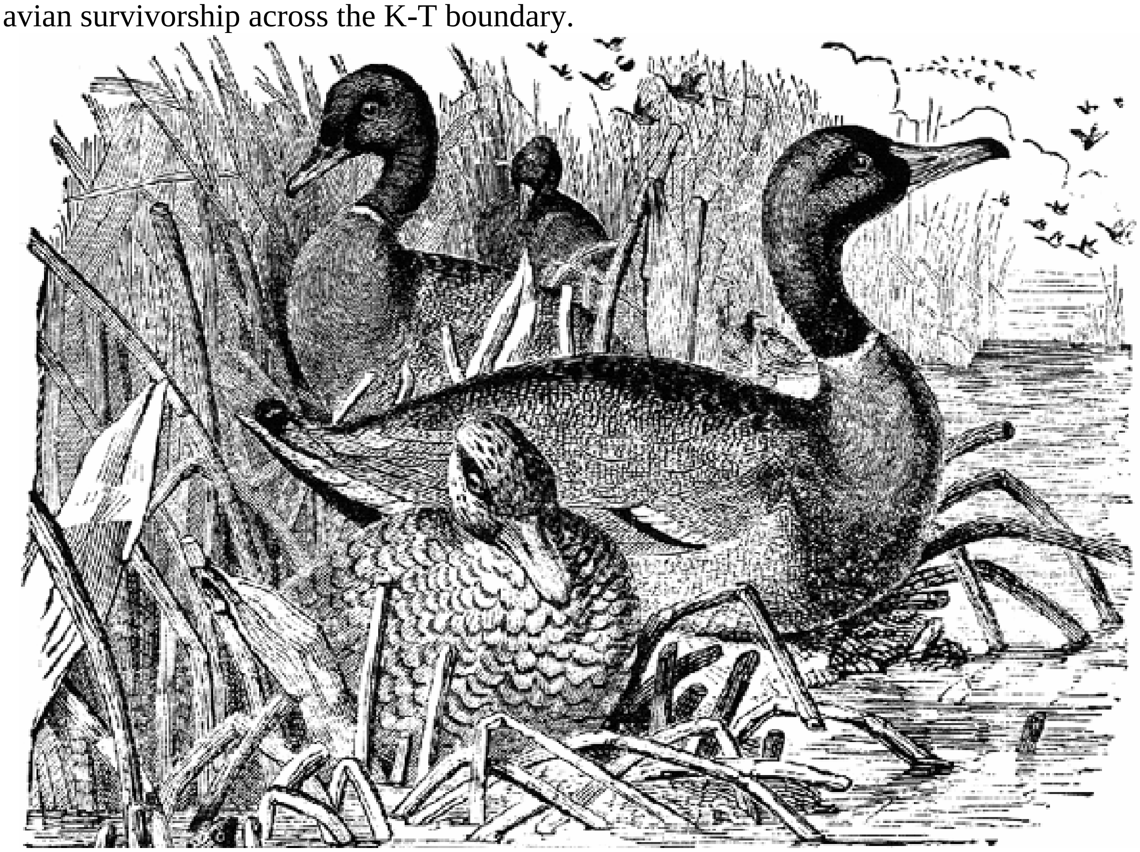

Figure 15.05 The anseriform lineage, which today includes ducks may be represented in the Late Cretaceous by a fossil known as *Presbyornis*.

Expert opinions on precise placements of Cretaceous birds on the avian map vary and are largely untested by phylogenetic analysis. Nevertheless, a consensus view is that four living lineages were present. The first is known as Anseriformes, which today includes about 151 species of ducks, geese, and screamers (fig. 15.05). Most anseriforms live and feed along the margins of bodies of water where they hunt for small animals and aquatic plants. With thick, water-proof plumage, anseriforms have navigated the world's oceans and waterways and are found over much of the world. Many are migratory, flying thousands of miles each year. Others have dwarfed forelimbs and are flightless. Many oceanic islands have endemic species, which live there and nowhere else. Fossil anseriforms have been found in marine and freshwater deposits throughout the Tertiary. From Late Cretaceous rocks of Vega Island, along the Antarctic peninsula, a fragmentary skeleton has been identified as *Presbyornis*[13], which is otherwise known from well-preserved Tertiary fossils. *Presbyornis* is thought to be either a relative of the ducks or a more primitive anseriform[14]. Another Cretaceous *Presbyornis* specimen is reported from Mongolia[15]. Only the fused metatarsal and ankle bones (the tibiotarsus) of one foot were found.

Figure 15.06 If the relationships of fossils from central Asian and the Antarctic peninsula are correctly mapped, then the lineage that included today's loons, like this Great Northern Diver, had achieved a global distribution by the end of the Cretaceous.

A second modern lineage whose path begins in the Cretaceous includes the four living species of modern loons - Gaviiformes[16]. Throughout their known history, loons have been waterbirds. Modern loons (fig. 15.06) are foot-propelled divers, whose hindlimbs resemble *Hesperornis* in mechanical design. Loons have pointed bills and torpedo-shaped bodies for efficient swimming. They chiefly eat fish, but also dine on other marine life. Unlike *Hesperornis*, loons retain powerful wings and can fly great distances. With dense, compact plumage they winter mostly at sea, living and feeding on the water for months at a time. The oldest fossil loon is *Neogaeornis wetzeli*, from the Late Cretaceous of Chile. This specimen was long mistaken for *Hesperornis*, until the U.S. National Museum's preeminent paleoornithologist Storrs Olson recognized it as a loon. Additional *Neogaeornis* material from Seymour Island, Antarctica, strengthens this identification. A third Cretaceous loon was recently discovered in Uzbekistan, from rocks about 20 million years older than *Neogaeornis*. If this identification is correct, then loons had dispersed widely across the globe long before the end of the Cretaceous.

Figure 15.07 This European avocet represents the charadriiform lineage, which unquestionably extends into the early Tertiary and may be represented by Cretaceous fossils.

The third Cretaceous lineage is Charadriiformes, which today includes a vast diversity of birds that spend most of their lives around water (fig. 15.07). Most modern charadriiforms migrate; most are strong flyers; and many can dive for food. They eat crabs, mussels, insects, fish, snails, lizards, seeds, and sometimes vegetation. The approximately 366 living charadriiform species represent many distinctive lineages and include auks, avocets, coursers, curlews, gulls, murres, oystercatchers, plovers, puffins, sandpipers, skimmers, stilts, terns, and woodcock among others. Not all were present in the Cretaceous, but nearly a dozen species have been named for Cretaceous fossils found in North America and Asia[17]. Owing to their incompleteness, and to revisions of age estimates for the rocks from which many of the fossils have come[18], these identification are possibly the most problematic and controversial among all the Cretaceous birds. However, they are unequivocally represented by fossils from the first 10 million years of the Tertiary.

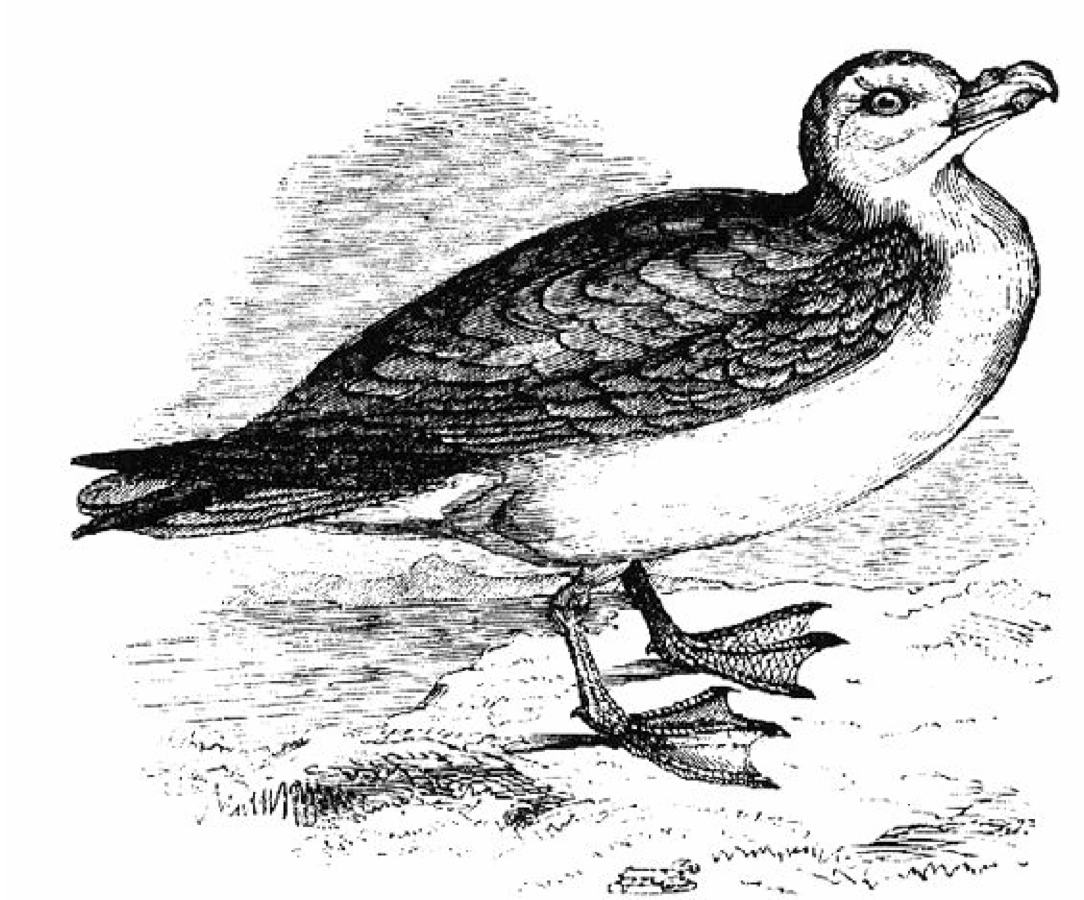

Figure 15.08 This fulmar represents the modern procellariiform lineage - the tube knoses. Notice the tube on the upper surface of the bill.

The fourth modern lineage represented by Cretaceous fossils is known as Procellariiformes - the tube noses - which includes the 92 living species of living albatrosses, shearwaters, and petrels (fig. 15.08). All of its modern members have hooked, deeply grooved bills with nostrils enclosed in a narrow tube that conveys excess salt secreted by the salt gland. With long, narrow pointed wings, they are excellent flyers. Some have very wide wing for soaring great distances over water. The wingspan of the albatross reaches 3.5 meters, the greatest of any living bird. The Cretaceous fossil record of procellariforms is widely acknowledged in the literature. But it seems to rest largely upon fragmentary wishbones from New Zealand and Mongolia[19].

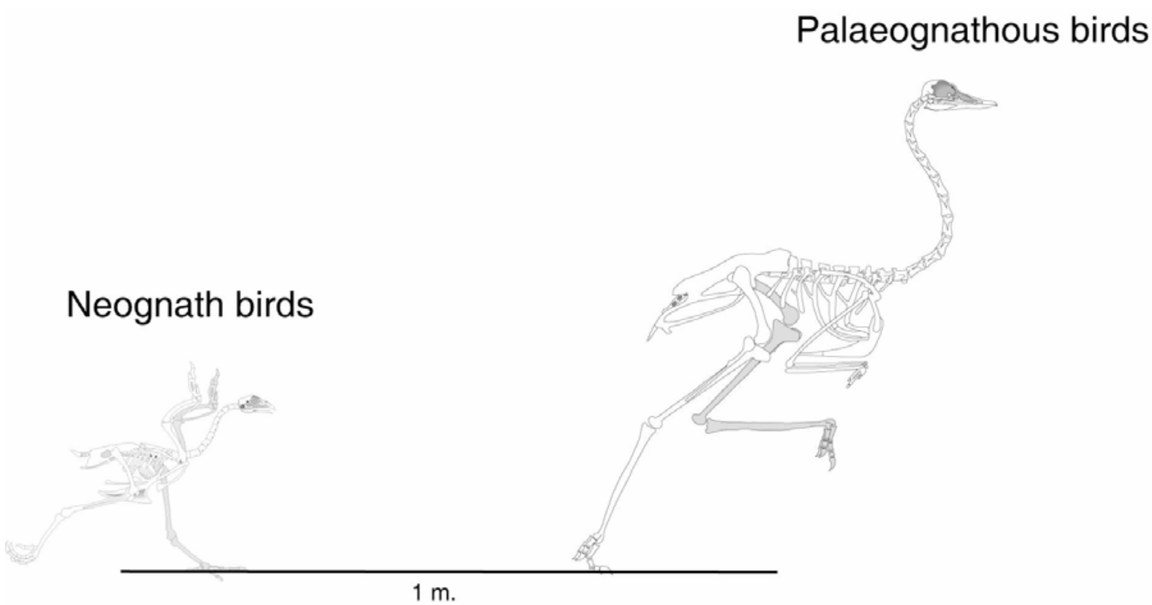

Figure 15.09 All living birds belong either the neognath lineage, represented here by the domestic chicken *Gallus gallus*, or to the palaeognath lineage, represented here by the rhea, *Rhea americana*.

Additional modern lineages identified from Cretaceous fossils include cormorants, pelicans, tropicbirds, flamingos, and relatives of chickens and turkeys, as well as others. But, while possible, these identifications are based on even less secure evidence than the four lineages just mentioned.

Adding ghost lineages that connect the known fossil species, provides a more accurate estimate the diversity of dinosaurs that crossed the K-T boundary than counting fossil species alone. Conservatively, if we accept as correct any one of the fossils now identified as anseriform, procellariiform, gaviiform, or charadriiform, then at least three major evolutionary paths of living birds were present in the Late Cretaceous. One of these is called Palaeognathae, which includes the modern ostriches and its relatives (fig.

15.09). The other is its sister lineage, Neognathae, which includes all other birds. Furthermore, the neognath lineage must have split into two distinct lines during the Cretaceous. The first includes the anseriforms plus the galliform birds (chickens, turkeys, and relatives). Its sister lineage includes all other neognathous birds.

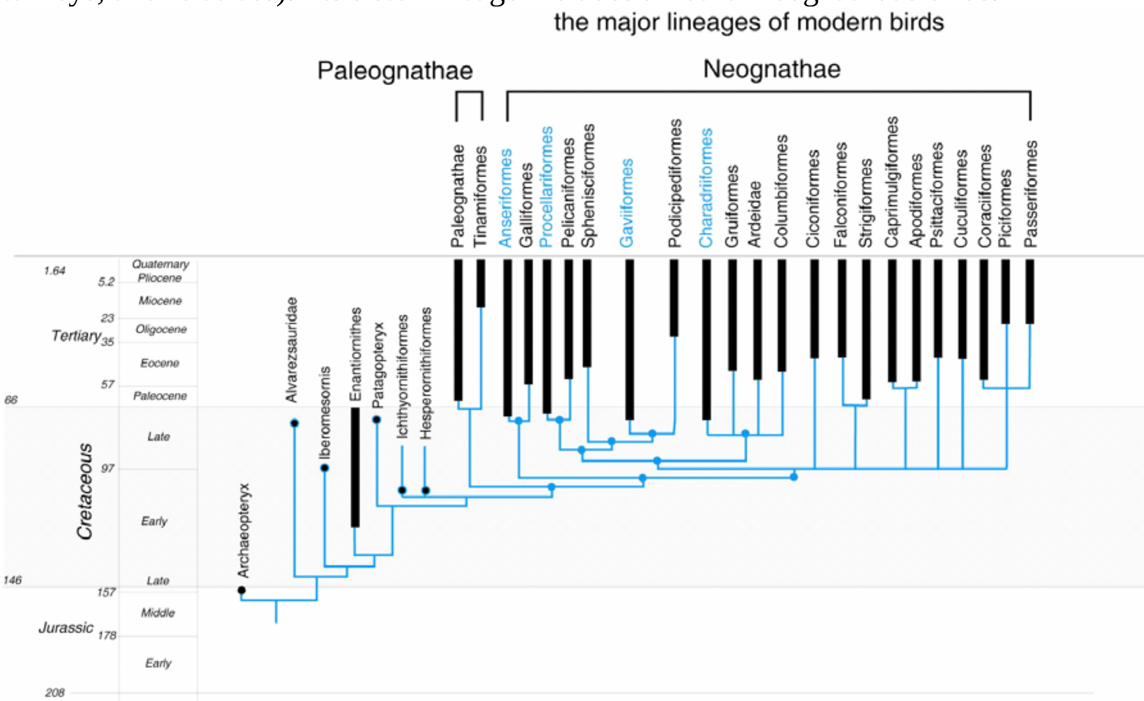

Figure 15.10 If this map of relationships is correct, then nearly 20 major living bird lineages may have crossed the K-T boundary, even though very few are known from Cretaceous fossils. (Phylogeny based on, Cracraft, J. 1988. The major clades of birds. Pp., 339-361, In: M. J. Benton (ed.), The Phylogeny and Classification of the Tetrapods, Systematics Association Special volume 35A, Oxford, Clarendon Press; and Chiappe, L., 1995. The first 85 million years of Avian Evolution. Nature, 378: 349-355.)

If all four of the alleged Cretaceous groups are correctly identified, then an additional dozen or more of today's major living lineages must have originated in the Cretaceous (fig. 15.10). One lineage includes many of today's large fish-eating birds - the greebs, loons, pelicans, frigate birds, gannets, cormorants, albatrosses and petrels. From what we know of their relationships, at least three of these must have split off before the loons. Another Cretaceous ghost lineage leads to today's pigeons, doves, cranes, herons, rails, gulls, auks, and other shorebirds. At least two evolutionary major trails had split for these birds during the Cretaceous. Another ghost lineage extending into the Cretaceous leads to the living raptorial birds the hawks, falcons, and owls. Still another leads to living swifts and humming birds, and still another least to living kingfishers, woodpeckers, toucans, and songbirds. It is hard to say how diverse any of these lineages had become in the Cretaceous - only that the stem lineages for a great diversity of living birds were present.

Alan Feduccia contends that the Cretaceous specimens are so incomplete that "regretfully, many must simply be ignored"[20]. But despite being incomplete, phylogenetic systematists argue that their positions on the map of Life can be generally plotted. After all, they can be identified as birds based on their hollow bones, the fused elements in the foot and ankle, and details of the shapes of the bone fragments. In some cases, they can be placed fairly precisely within Aves, fulfilling the aim of phylogenetic analysis. A major weakness of Feduccia's Phoenix hypothesis is that it fails to account for much of the Cretaceous fossil bird record.

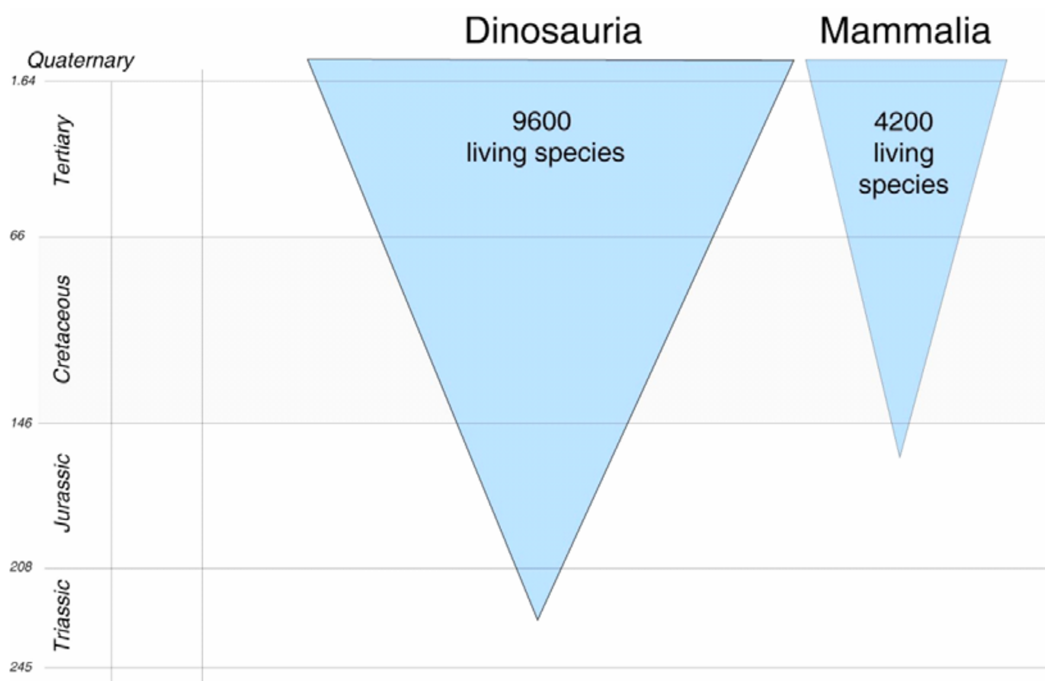

Figure 15.11 From the general shapes of their histories of diversification, it is evident that the Age of Mammals played out its entire history in the shadow of dinosaurs.

Even if we were to accept Feduccia's claim that most of the Cretaceous birds are too fragmentary to identify accurately, still other new mapping techniques trace the ghosts of many living bird lines into the Mesozoic. Alan Cooper (Victoria University, New Zealand) and David Penny (Massey University, New Zealand) examined the question of bird survivorship across the K-T boundary[21], by comparing DNA sequences from pairs of modern birds whose relationships were uncontroversial, using the differences in sequence as a proxy for the rates of evolutionary divergence. They calibrated the speed of evolutionary change using a well-established early Tertiary fossil record for the lineages. The only Cretaceous identification Cooper and Penny accepted was that of a loon, and even this identification was not critical to their results.

From these calibrated speed estimates, Cooper and Penny calculated the minimum divergence time of the two members for each pair. By combining distantly related pairs of birds into quartets, they estimated the minimum divergence times between the pairs, and further refined age estimates for the original pair-wise comparisons. These were conservative estimates because if errors were made regarding relationships - if the pairs were more closely related than they thought - it would result in an artificially young divergence date. In addition to the lineages listed above, Cooper and Penny estimated that the parrot lineage and the passeriform lineage - which includes several thousand living species of perching birds and song birds - were both present in the Cretaceous and survived to the present.

At the Boundary

When all the available evidence from ghost lineages is taken into account, it looks like both birds and mammals had diversified and become globally distributed by the end of the Cretaceous. But what happened at the K-T boundary? Was there a catastrophic loss of diversity?

Let's look first at the record for mammals. As we saw in Chapter 7, only a few localities preserve vertebrate-bearing sedimentary rocks just above and below the K-T boundary, and all are in western North America. The most complete sequences of terrestrial rocks leading up to the boundary are in Montana and southern Alberta, where we can track species that were fossilized in rocks of the Judith River Formation into the overlying Hell Creek Formation. These two formations intermittently span the last 10 million years of the Cretaceous.

Dave Archibald and William Clemens have shown that in this region, the marsupials, which today include the kangaroos, opossums, and other pouched mammals, were hardest hit. Only one of eleven marsupial species present in the Cretaceous survived into the Tertiary. Archibald points out that marsupial fossils are rare, so sampling artifacts may significantly inflate the severity of loss[22]. Marsupials disappeared altogether from North America very early in the Tertiary, but elsewhere, marsupials evolved into about 259 living species plus abundant extinct Tertiary species that have been found in many parts of the world. Given their success elsewhere, it is doubtful that the K-T loss of marsupial diversity in North America was representative of the rest of world, but without more evidence we can only speculate.

Rodent-like multituberculates were present in the Late Jurassic and Cretaceous, and had a global distribution. In North America, only 50% of the Cretaceous multituberculate species survived into the Tertiary. Locally at least, this group also took a big hit, but elsewhere in the world, the Tertiary record of multituberculates is not well known. So the loss at the boundary in Montana may or may not represent global diversity trends. Multituberculates survived in the Northern Hemisphere for 20 million years after the K-T extinctions before finally disappearing in the mid-Tertiary.

The placentals comprise about 93% of modern mammalian diversity. By Archibald's estimates they were not affected. We noted earlier that only one of the six placental species found in the Cretaceous went extinct; five of the six survived. Furthermore, Archibald argues that the extinct Cretaceous species actually evolved into a Paleocene species, producing what he calls pseudoextinction in which there was no loss of net diversity. Based on what is known of placental relationships in general, there must have been a greater diversity of placentals present elsewhere in the world.

Overall, in western North America as many as 55% of the mammalian species may have gone extinct, but it is impossible to say that this number is representative of the world. It is clear that mortality was highly selective and varied from lineage to lineage. Available data indicate that placentals, which spawned the vast majority of post-Cretaceous mammalian species, were largely unaffected at the K-T boundary.

How did Dinosauria fare at the K-T boundary? Most paleontologists agree that the non-avian dinosaurs all became extinct at or before the end of the Cretaceous, despite occasional claims to the contrary[23]. The evidence for their post-Cretaceous survival consists almost entirely of isolated teeth from rocks as much as 10 million years younger than the boundary. But all the physical evidence points to these rare teeth being reworked from older Cretaceous deposits. In every case, the teeth consist of isolated, worn and broken specimens with abrasions that record an extensive history of transport by water. Reworking is a common geological process, and dinosaur teeth are the densest and most durable parts of the skeleton. As the younger Paleocene streams cut down into underlying Cretaceous sediments, they occasionally exhumed older remains, breaking them up and abrading them by tumbling the pieces further downstream before their second burial. The alleged Paleocene teeth are always more worn than the teeth collected directly from Cretaceous rocks, and no articulated skeletal parts have been found in Paleocene rocks. Without stronger evidence, it looks like all the non-avian dinosaurs went extinct at or before the end of the Cretaceous.

Was their extinction rapid or gradual? Many paleontologists have now spent numerous field seasons trying to answer questions about changes in dinosaur diversity.

The pace of discovering new species is now slowing, and the current picture is more complete than for any other region preserving a comparable time slice. Despite the completeness, there are conflicting interpretations.

As noted earlier, David Fastovsky (University of Rhode Island) and Peter Sheehan (University of Wisconsin) interpreted their evidence from the latest Cretaceous Hell Creek Formation to be consistent with a geologically instantaneous extinction of all the non-avian dinosaurs, along with 88% of the terrestrial tetrapods found in the Cretaceous[24]. However, Archibald and Laurie Bryant (now at the Bureau of Land Management) measured dinosaur diversity by surveying a broader time span, combined with a more fine-scaled stratigraphic sequence, and came to a different answer[25]. They tabulated a minimum of 32 species of non-avian dinosaurs in the Judith River Formation, but in the overlying Hell Creek Formation there are only 19 species-- a 40% decline in the diversity of non-avian species during the 10 million years leading up to the K-T boundary. The proportion of this decline was greatest among ornithischians, with roughly 66% of these species disappearing before the end of the Cretaceous. But only about 25% of the non-avian saurischians disappeared during this 10-million-year interval. There is evidence to suggest that the 19 non-avian dinosaur species from the Hell Creek died out in a very short time near the boundary. So, in western North America, the end for some species of non-avian dinosaurs may have been relatively quick, but their numbers had apparently been waning for several million years before the end of the Cretaceous. Whether this pattern represents the rest of the world is uncertain. Globally, there are approximately 120 named species of non-avian dinosaurs that can be accounted for during the last 10 million or so years of the Cretaceous[26], but we do not know exactly when within this interval most of them died out.

Among avian dinosaurs, there simply were not enough specimens represented in the Berkeley collections for Archibald and Bryant to meaningfully estimate changes at the boundary. On a global scale, the Hesperornithiformes and Ichthyornithiformes were evidently gone five million years before the end of the Cretaceous. Feduccia’s picture of a catastrophic extinction at the end of the Cretaceous is distorted because he failed to account for significant losses of avian diversity leading up to the boundary. Alvarezsaurids, Enantiornithines, and a few others made it to the end of the Cretaceous, or nearly so, but no further. But despite the losses leading up to and at the boundary, a dozen or so separate lineages of living birds trace their origins back across the K-T boundary, and must have survived whatever happened at the end of the Cretaceous. The available data suggest that the adaptive radiation of birds was well under way before the Mesozoic ended.

The Bottom Line

From a modern phylogenetic perspective, dinosaurs not only crossed the K-T boundary, they survive today in great abundance. But even though our understanding of dinosaur history has radically shifted, some other things have remained the same. As in the 19^{th} Century, many implications of the theory of evolution seem to be overlooked by the proponents of the theory of homoplasy. Some scientists still reject that birds are related to dinosaurs, arguing that the similarities in both ontogeny and phylogeny reflect convergent evolution. However, they offer no well-founded alternative hypothesis of relationship. If birds are not dinosaurs, then where do they fit on the tree of Life? Although claiming to be evolutionists, these scientists use methods that were championed a century ago by anti-Darwinians seeking to discredit the theory of evolution. Without a body of supporting anatomical or genetic evidence, saying that birds evolved independently is little different from saying that they were separately created.

There are similarities in the patterns of diversification for birds and mammals (figure 15.12). But the patterns measured with phylogenetic maps suggest that both lineages originated long before the Mesozoic ended and steadily increased their diversity far into the Tertiary. The jury is still out in deciding exactly what happened at the K-T boundary. So diverse were birds and mammals by the Late Cretaceous that meaningful estimates of changes in diversity across the K-T boundary will only come with path-by-path analyses, when the individual evolutionary trails are mapped in greater detail and as more fossils are recovered.

Alan Feduccia wrote an influential book whose title, *The Age of Birds*, conveys the important point that birds have outnumbered mammals throughout the Cenozoic. But he overlooks that, from the Triassic to the present, dinosaurs have *always* been represented by more species than mammals. The Age of Dinosaurs is not over yet.

References for Chapter 15

1) Weishample, D., P. Dodson, and H. Osmolska 1990. The Dinosauria. Berkeley, University of California Press.

2) Feduccia, A. 1995. Explosive evolution in Tertiary birds and mammals. Science, 267:637-638; Feduccia, A., 1996. The Origin and Evolution of Birds. New Haven, Yale University Press.; Hou, L., L. D. Martin, Z. Zhou, A. Feduccia, Early adaptive radiation of birds: evidence from fossils from northeastern China. Science, 274: 1164-1167.

3) Cracraft, J. 1981. Toward a phylogenetic classification of the Recent birds of the world (Class Aves). Auk 98:681-714; Cracraft, J. 1986. The origin and early diversification of birds. Paleobiology 12:383-399; Cracraft, J. 1988. The major clades of birds. Pp., 339-361, In: M. J. Benton (ed.), The Phylogeny and Classification of the Tetrapods, Systematics Association Special volume 35A, Oxford, Clarendon Press.

4) Chiappe, L., 1995. The first 85 million years of Avian Evolution. Nature, 378: 349-355.

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

6) Norell, M. A., 1992. Taxic origin and temporal diversity: the effect of phylogeny. Pp. 89-118, In: M. J. Novacek and Q. D. Wheeler (eds.), Extinction and Phylogeny. New York, Columbia University Press; Norell, M. A., 1993. Tree-based approaches to understanding history: comments on ranks, rules, and the quality of the fossil record. American Journal of Science 293-A: 407-417.

7) Owen, R. 1839. Observations on the fossils representing the Thylacotherium prevostii, Valenciennes, with reference to the doubts of its mammalian and marsupial nature recently promulgated; and on the Phascolotherium bucklandi. Geological Transactions, Series 2, vol. VI: 186-265; Owen, R. 1971. Monograph of the fossil Mammalia of the Mesozoic formations. London, Paleontographical Society Monograph 24. 115pp.

8) Lillegraven, J. A., Z. Kielan-Jaworowska, and W. A. Clemens, 1979. Mesozoic Mammals: the first two-thirds of mammalian history. Berkeley, University of California Press; Szalay, F. S., M. J. Novacek, and M. C. McKenna, 1993. Mammal Phylogeny. New York, Springer Verlag.

9) Jenkins, F. A., Jr., S. M. Gatesy, N. H. Schubin, and W. W. Amaral, 1997. Haramiyids and Triassic mammalian evolution. Nature, 385:715-718.

10) Nessov, L. A. 1987. Results of search and study of Cretaceous and early Paleocene mammals on the territory of the USSR. Ezhegodnik Vsesoyuznovo Paleontologicheskovo Obschestva 30: 199-219 [in Russian]; see also a review of

this work in: Archibald, J. D. 1996a. Dinosaur Extinction and the end of an era. New York, Columbia University Press.

11) Archibald, J. D. 1996b. Fossil evidence for a Late Cretaceous origin of “hoofed” mammals. Science 272:1150-1153.

12) Archibald, J. D. 1996a. Dinosaur Extinction and the end of an era. New York, Columbia University Press.

13) Noriega, J. I., and P. Tambussi 1995. A Late Cretaceous Presbyornithidae (Aves: Anseriformes) from Vega Island, Antarctic Peninsula: paleobiogeographic implications. Ameghiniana 32:57-61.

14) Olson, S. L., 1985., The fossil record of birds. Pp. 79-252, In: D. S. Farner, J. R. King, and K. C. Parkes (eds.) Avian Biology, volume 8; Olson, S. L. 1994. A giant Presbyornis (Aves: Anseriformes) and other birds from the Paleocene Aquia formation of Maryland and Virginia. Proceedings of the Biological Society of Washington, 107:429-435; Ericson, P. 1992. Evolution and systematic elements of the Paleogene family Presbyornithidae. Frankfurt III Symposium Society of Avian Paleontology and Evolution, 1: 16.

15) Kurochkin, E. V. 1995. The assemblage of Cretaceous birds in Asia. Pp. 203-208, *in*: Sixth symposium on Mesozoic Terrestrial Ecosystems and Biota, A. L. Sun (ed.) Beijing, China Ocean Press.

16) Olson, S. L. 1992. *Neogaeornis wetzeli* Lambrecht, a Cretaceous loon from Chile. Journal of Vertebrate Paleontology, 12:122-124.

17) Olson, S. L., 1985., The fossil record of birds. Pp. 79-252, In: D. S. Farner, J. R. King, and K. C. Parkes (eds.) Avian Biology, volume 8.

18) Olson, S. L., and D. Parris 1987. The Cretaceous birds of New Jersey. Smithsonian contributions to Paleobiology 63:1-22.

19) Olson, S. L., 1985., The fossil record of birds. Pp. 79-252, In: D. S. Farner, J. R. King, and K. C. Parkes (eds.) Avian Biology, volume 8; Kurochkin, E. V., 1995. The assemblage of Cretaceous birds in Asia. Pp. 203-208, *in*: Sixth symposium on Mesozoic Terrestrial Ecosystems and Biota, A. L. Sun (ed.) Beijing, China Ocean Press.

20) Feduccia, A., 1996. The Origin and Evolution of Birds. New Haven, Yale University Press. Page 165.

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

22) Archibald, J. D. 1996a. Dinosaur Extinction and the end of an era. New York, Columbia University Press.

23) Archibald, J. D. 1996a. Dinosaur Extinction and the end of an era. New York, Columbia University Press.

24) Fastovsky, D. E., and P. M. Sheehan, 1994. Habitat vs. asteroid fragmentation in vertebrate extinctions at the KT boundary: The good, the bad, and the untested. In: New Developments regarding the KT event and other catastrophes in Earth history. Lunar and Planetary Institute Contribution 825: 36-37.

25) Archibald, D. E. and L. Bryant. 1990. Differential Cretaceous-Tertiary extinctions of nonmarine vertebrates: evidence from northeastern Montana. Pp. 549-562 In V. L. Sharpton and P. Ward (eds.) Global Catastrophes in Earth History: An Interdisciplinary Conference on Impacts, Volcanism, and Mass Mortality. Geological Society of America Special Paper 247.

26) Weishample, D., P. Dodson, and H. Osmolska 1990. The Dinosauria. Berkeley, University of California Press.

Figure Captions for Chapter 15

Figure 15.01 Alan Feduccia's controversial hypothesis about the history of avian diversity depicts an episode of Mesozoic diversification that was nearly chopped off at the K-T boundary. The catastrophic extinction was followed by an "explosive" Tertiary radiation of modern birds from a small group of survivors.

Figure 15.02 If this map is correct, that living lineages 1 and 2 are sisters, then both must have been present in the Cretaceous, and both must have survived across the K-T boundary. Although we have found no fossils for lineage 1 and have no idea of just how diversified it was in the past, we can connect its history in time to lineage 1, which did leave a fossil record. Crosses denote extinct species.

Figure 15.03 Mesozoic mammals were rarely larger than the modern opossum, and they left little to the fossil record besides isolated jaws and teeth, the hardest parts of the skeleton.

Figure 15.04 The solid black lines indicate the range of each lineage, based on known fossils. The blue lines are ghost lineages that represent the approximate duration in time for each lineage, based on what we know about their relationships (based on Archibald, J. D. 1996b. Fossil evidence for a Late Cretaceous origin of "hoofed" mammals. Science 272:1150-1153.)

Figure 15.05 The anseriform lineage, which today includes ducks may be represented in the Late Cretaceous by a fossil known as *Presbyornis*.

Figure 15.06 If the relationships of fossils from central Asian and the Antarctic peninsula are correctly mapped, then the lineage that included today's loons, like this Great Northern Diver, had achieved a global distribution by the end of the Cretaceous.

Figure 15.07 This European avocet represents the charadriiform lineage, which unquestionably extends into the early Tertiary and may be represented by Cretaceous fossils.

Figure 15.08 This fulmar represents the modern procellariiform lineage - the tube noses. Notice the tube on the upper surface of the bill.

Figure 15.09 All living birds belong either the neognath lineage, represented here by the domestic chicken *Gallus gallus*, or to the palaeognath lineage, represented here by the rhea, *Rhea americana*.

Figure 15.10 If this map of relationships is correct, then nearly 20 major living bird lineages may have crossed the K-T boundary, even though very few are known from Cretaceous fossils. (Phylogeny based on, Cracraft, J. 1988. The major clades of birds. Pp., 339-361, In: M. J. Benton (ed.), The Phylogeny and Classification of the Tetrapods, Systematics Association Special volume 35A, Oxford, Clarendon Press; and Chiappe, L., 1995. The first 85 million years of Avian Evolution. Nature, 378: 349-355.)

Figure 15.11 From the general shapes of their histories of diversification, it is evident that the Age of Mammals played out its entire history in the shadow of dinosaurs.