Chapter 16
Diversification and Decline

The period from the mid-Cretaceous to the end of the Tertiary witnessed an unprecedented diversification among vertebrates, as the world became populated by thousands of species of birds. One recent encyclopedic treatment, by Charles Sibley and Burt Monroe of Yale University, lists 9,672 living species[1]--about ten times the number of known Mesozoic dinosaurs. However, archeological research is revealing that today's avian diversity is well below its peak, and that several thousand more species were alive just a few thousand years ago. But before examining the portentous recent losses, we survey the historic diversification of birds and investigate the circumstances behind the greatest exploitation of the land and sky by any vertebrate. An appreciation for the history of diversification of living birds will help to clarify a series of mass extinctions possibly more severe than the one at the K-T boundary for the dinosaur lineage.

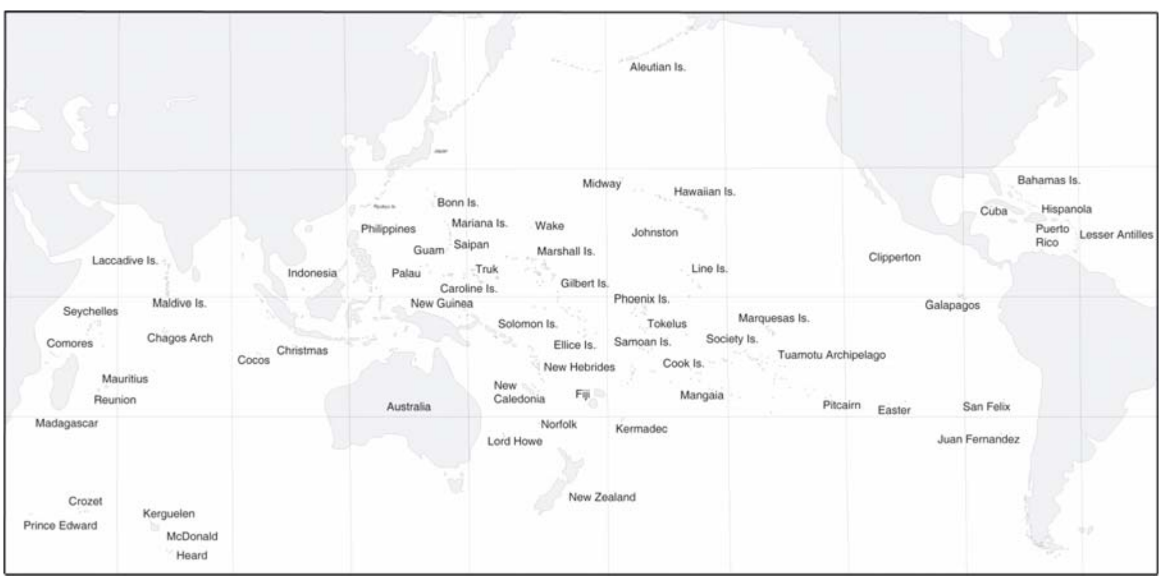
Isolation and Diversity

Multitudinous organisms populate the world today, most of whom originated through different modes of *speciation*. Speciation is the great producer of diversity. In the case of birds and most other tetrapods, speciation involved geographic isolation of small populations followed by reproductive isolation. All birds reproduce sexually, like most other vertebrates, and this helps drive diversification. Apart from identical twins, every individual is different, with its own complement of DNA, and every individual has its own unique history in time and space. But as long as the members of a population or different populations can potentially interbreed, gene flow among them has a homogenizing effect from generation to generation. Over time, the boundaries of variability may grow, shrink, or drift, yet we are still left with a single species.

But if two populations become geographically isolated from each another in a way that prevents gene flow, each population has a smaller gene pool than before. Over time, the populations become increasingly different. Through natural selection and genetic drift, descendants are modified in response to their hereditry and environmental circumstances, as genes are mixed from generation to generation. With sufficient time, the populations diverge to the point that, even if they were to again share overlapping territory, they would probably not successfully interbreed. Where before there was only one species, there are now two. Each has its own distinct geographic range, and these ranges do not usually overlap. The diversification of birds is dominated by patterns indicating a history of geographic isolation and speciation. In turn, this history is intricately tied to the dynamic history of the Earth's crust and climate.

The most fertile regions for the adaptive radiation of new bird species have been the islands of the eastern Pacific and Indian Oceans, as well as the forests of the Andes and great Amazon Basin (fig. 16.01). Other regions around the Pacific rim, like western North America and southeastern Asia, were also great centers of diversification. Many of these regions have *endemic* bird species--native forms confined to a small region. But they also host migratory and wide-ranging species. Each island or patch of forest can host its own unique assemblages of fauna and flora.

In the first part of the book, Cretaceous volcanism was implicated as a possible cause for K-T extinctions. This same volcanism may also have been responsible for much of the avian diversity that evolved on both sides of the K-T boundary. Recall that heat emanating from the Earth's core generates convective plumes of magma that rise through the mantle and disrupt the overlying crust in tectonic movement. Between 120 and 125 million years ago, a superplume of hot magma boiled away from near the Earth's molten outer core, rising through mantle below what is now the western Pacific. As the superheated upwelling approached the surface, the most volatile components erupted through the ocean floor, creating submerged volcanoes and mountain ranges that spread over much of the Pacific basin[2]. The tips of these peaks are the seamounts and volcanic islands of Polynesia, Melanesia, Micronesia, the Malay Archipelago, and others of the region. Many of these islands have their own unique species of birds.



Oceanic islands typically emerge above the waves rather barren and lifeless. But with time, they provide unique opportunities for colonization. Lichen and fern spores reach their shores quickly with the wind. Their roots churn organic material into the volcanic rubble, and soils eventually accumulate. Many islands develop a rich substrate that sustains great floral diversity. And with the base of the food chain established, the way is paved for the influx of herbivores and carnivores[3]. From the mid-Cretaceous onward, islands began to emerge from the waves, like new condominiums awaiting their first residents.

There are numerous ways for tetrapods to cross salt water barriers and reach emerging islands, but the happenstance process of island colonization means that each island may be unique. A few species can withstand the trip through salt water and float or swim to the islands that they colonize. Tortoises probably floated to the island chains, like the Galápagos and Aldabra islands, where they evolved to giant size and each island became home to its own distinctive population. Spiders diversified enormously on islands. As tiny juveniles, they can balloon on air currents with a strand of spun silk for vast distances. They have been collected at altitudes above 30,000 feet in the aerial plankton by planes towing net-like windsocks. Insects hitch rides with birds and other travelers. Bats also fly onto islands, carrying parasites and seeds of the fruits they eat. Seals and sea lions swim to islands. Rafts of branches, logs, or vegetation mats wash out to sea with storm tides, complete with microorganisms, insects, and small vertebrates. But few mammals or lizards, and virtually no amphibians have successfully crossed wide saltwater barriers, without human help. Birds have been far more successful, flying or swimming out to fish in enriched coastal waters or island lakes.

A *continental island* is one that separated from its parent continent by tectonic forces or rising sea levels, isolating a sample of the biota found on the mainland. Madagascar is a continental island, whose isolation began nearly 70 million years ago, producing fantastic variations on African species present at the time of separation. Whole continents have become islands, following the break-up of Pangea during the Mesozoic. South America was an island for much of the Tertiary, until it became tied to North America at the isthmus of Panama. India was also an island for tens of millions of years, before colliding with Asia and creating the Himalayas. Australia still is an island. During isolation, each continent evolved a unique assemblage of bird species.

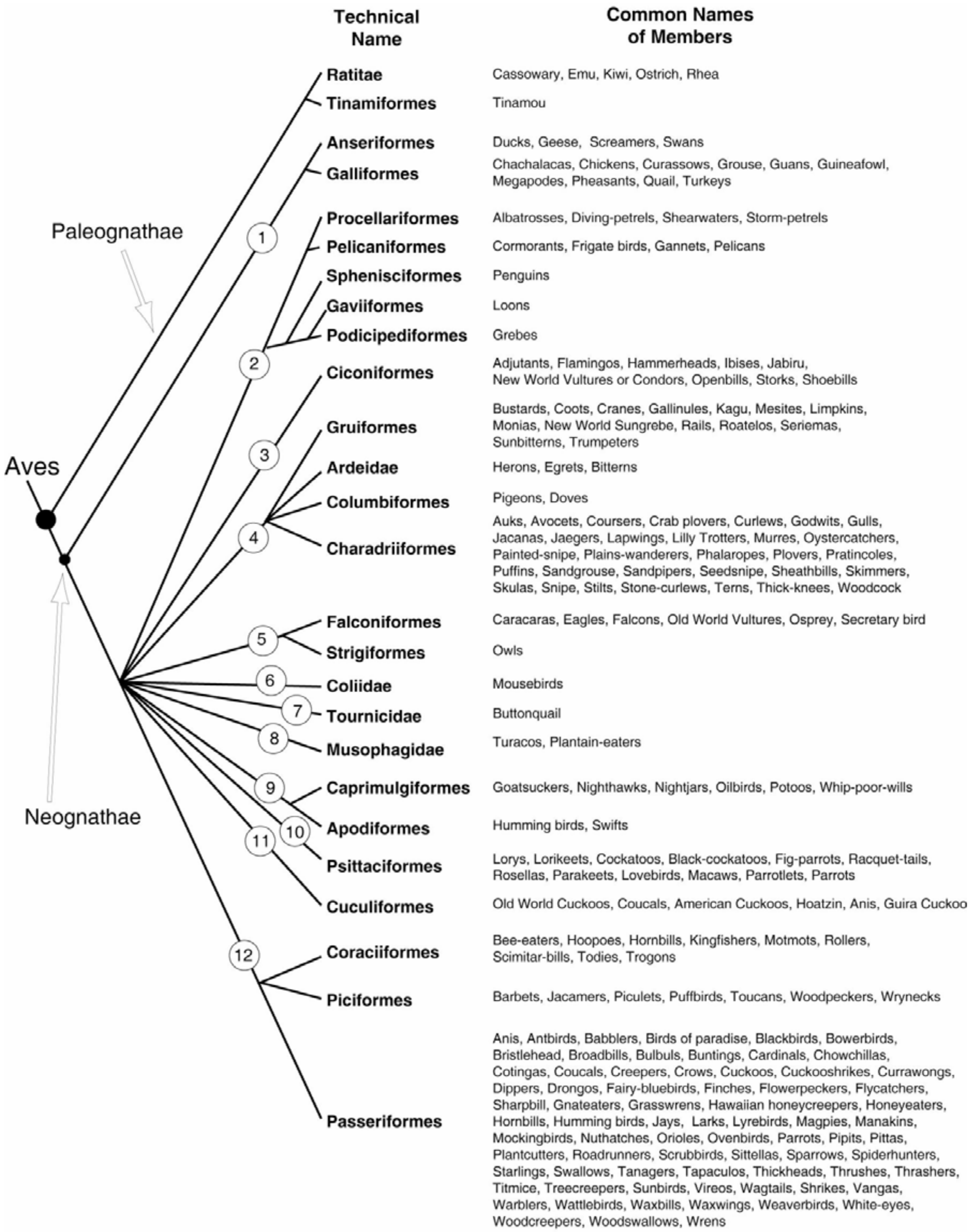
Tectonic activity on the eastern side of the Pacific basin catalyzed biotic effects via the formation of the Andes of South America and the Sierra Nevada of North America. Increased elevations along the western edges of these continents disrupted more uniform habitats and generated greater habitat diversity. The shallow Cretaceous seas that had covered North America and Asia receded, opening new lands to pioneering species. Novel terrestrial communities arose as the seabed emerged. In the forests and mountains, species could become isolated as a fire or a river shifting its course separated previously continuous populations of organisms in two. Many tropical forest birds will not cross open water even though they have the strength to do so. Vegetation and rainfall shifts due to elevation changes also partition the environment into different island-like zones and foster speciation among birds. From the mid-Cretaceous onward, the crust in and around the Pacific basin presented a huge, rapidly changing landscape that became the world's greatest center of bird diversification over the next 100 million years.

Diversity Rising

By far the greatest adaptive radiation was among the small terrestrial birds in forests and woodlands on continents and islands. But waterfowl, shore birds, and wading birds also became highly diversified, leaving the best Tertiary fossil record. Many shorebirds nest in great colonies, and some spectacular fossil localities have produced tens of thousands of their bird bones. But overall, the pace of Tertiary evolution among the seabirds has been slower than that of their woodland cousins, possibly because water birds are generally strong and wide-ranging flyers. The phylogenetic map for modern birds (fig. 16.02) is still under construction, and there is a big knot of unresolved relationships among several of its major pathways. Some major lineages have proper names, which we will introduce. For the rest, we will simply number them, and briefly describe their diversity and history.

Paleognath Birds

Two major evolutionary pathways trace back to the ancestral species of Aves[4]. These are Palaeognathae and Neognathae, which together contain all living birds[5]. Palaeognathae includes the ratite (Ratitae) lineage – the ostrich, which is the most massive and tallest of living birds (16.03), and ten related living species, plus a host of extinct relatives. All are flightless, terrestrial birds, with reduced forelimbs, huge egg-shaped bodies, powerful legs, and small heads perched atop long necks. The islands of New Zealand, Madagascar and the island continents of Australia and South America have each fostered endemic ratite species. Ornithologists long debated whether the ancestor of ratites could fly. Judging from their position on the evolutionary map of dinosaurs, we can see that all of the closest living relatives of ratites can fly, as did a host of their closest extinct relatives. Ratites have a fused wrist and hand plus a short pygostyle tail like other ornithothoracine birds, the back-turned pubis of maniraptorans, the long neck of



saurischians, and so on. This hierarchy of evolutionary features suggests that the ancestral bird could fly, and that some of its ratite descendants became flightless secondarily.

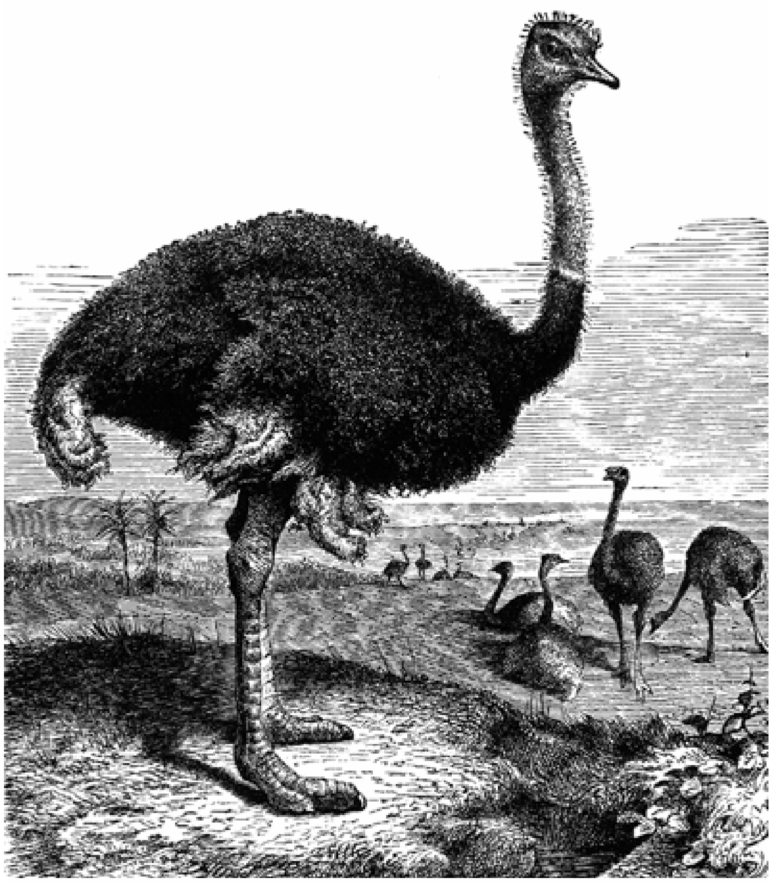


Figure 16.03 Dingus & Rowe

The tinamous (Tinamiformes) form a second pathway on the paleognath lineage, and their history reflects another adaptive radiation throughout varied grass- and woodland habitats (fig. 16.04). There are 43 living tinamous species, which are confined to the region from southern Mexico to Patagonia[5]. Given that ratites can't fly and that the flying tinamous are restricted to South America, it is difficult to explain the geographic distribution of the living palaeognath species as a result of migration or aerial dispersal. We should expect to see fossils in North America and Asia, documenting their passage between Africa, South America, and the Australian region. Despite several false alarms, no such fossils have been found. The geographic pattern of ratite distribution resembles that of many insects and plants--a *Gondwanan distribution*--where formerly continuous populations became fragmented and separated by the Mesozoic breakup of the southern supercontinent Gondwana. Geography provides additional evidence of the great antiquity of the palaeognath lineage.

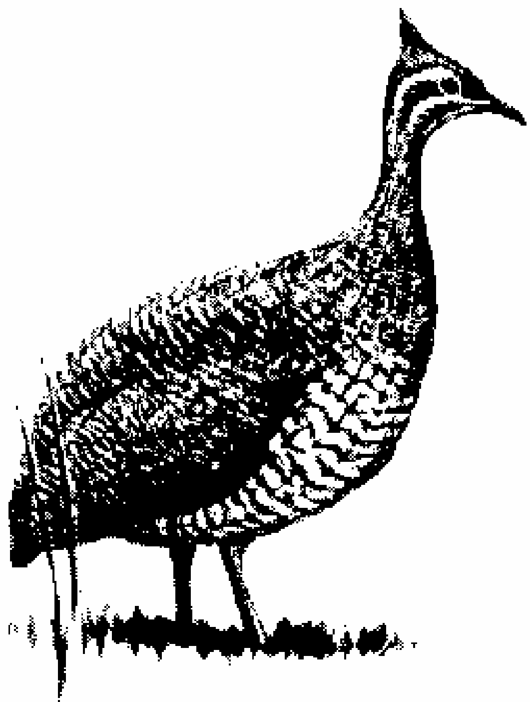


Figure 16.04 Dingus & Rowe

Neognaths

All other birds are members of the neognath lineage. Our current phylogenetic map depicts twelve major living lineages that trace back to the ancestral neognath. The relationships among these major pathways are not well understood, however. In many cases the individual lineages are highly distinctive. Parrots, for example, are rarely confused for some other type of bird, because a large gap separates parrots from all the others. The oldest parrot fossils are from the Eocene - about 50 million years ago - but they are already distinctly parrot-like[6]. This points to an even earlier time of origin, and no known fossils bridge that gap. Older, more primitive fossils of parrots, as well as the other eleven neognath pathways, are needed to fully resolve the map for this part of avian history.

Pathway 1 includes two sister lineages. We met Anseriformes – the ducks and geese -- in the last chapter. Its sister lineage, Galliformes, represents a radiation into the forests, brushlands, and grasslands, of the world (fig. 16.05). There are 293 living species[7], who mostly spend their lives on the ground where they hunt seeds, fruits, berries, insects, worms, and small vertebrates. Their flight is powerful but not prolonged. The oldest galliform fossils are from the Early Eocene of Wyoming[8]. However, their sister lineage, Anseriformes, includes the Cretaceous species *Presbyornis*. If *Presbyornis* is correctly mapped as a member of Anseriformes, then the entire galliform line must extend back into the Cretaceous as well.

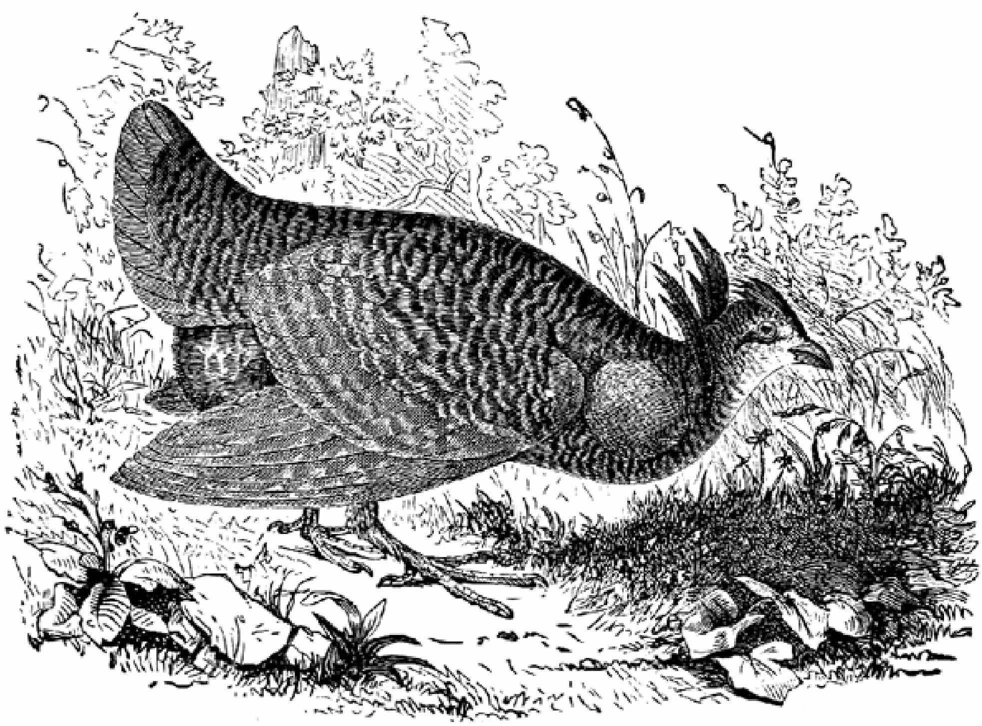


Figure 16.05 Dingus & Rowe

Pathway 2 leads to four major branches of birds that live in and adjacent to water. The pelicans (Pelicaniformes) are mostly wide-ranging birds that inhabit temperate and tropical zones (fig. 16.06). Also belonging to this lineage are Frigate birds, comorants, and gannets. Pelicaniformes are generally distinguished by long bills that support a pouch of skin that hangs below the jaw and neck for carrying food to their young. Nearly every species in the lineage is a strong flier with large wings. Pelicans are among the largest living birds, with bodies nearly six feet in length, with a wingspan close to ten feet. There is one flightless member of the lineage, the Galapagos Islands cormorant, which has dwarfed wings and lives along the island coasts. A fossil cormorant was reported from Late Cretaceous sediments of southern Mongolia[9], but the identification of this specimens has yet to be verified. Fossils are abundant from the Eocene onwards.

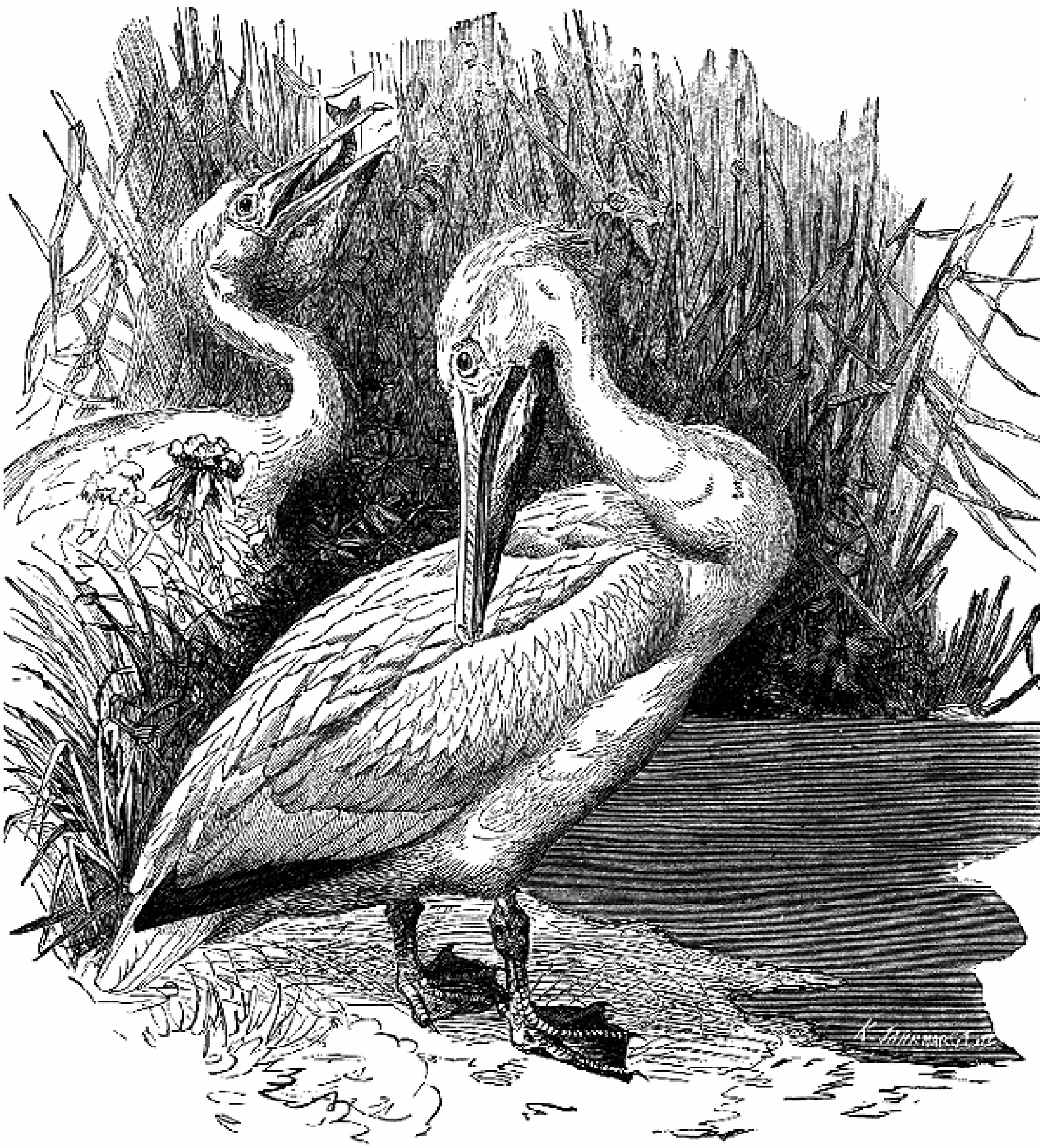


Figure 16.06 Dingus & Rowe

The seventeen species of living penguins (Sphenisciformes)[10] represent another trail on pathway 2 (fig. 16.07). Penguins hunt the southern oceans for fish, squid, and shrimp, 'flying' with powerful short wings through the water with spectacular dexterity.

The earliest fossils are from the Eocene of Seymour Island, Antarctica, and the entire history of the penguin lineage appears to have played out in the Southern Hemisphere. Two other trails branching from pathway 2 are the loons (Gaviiformes), who we met in the last chapter, and their cousins the grebes (Podicipediformes). Twenty-one grebe species can be found today worldwide (fig. 16.08), including several island endemics. The Colombian grebe is flightless and its geographic range is - or was - confined to a few ponds and lakes in the Andes. This species is probably now extinct.

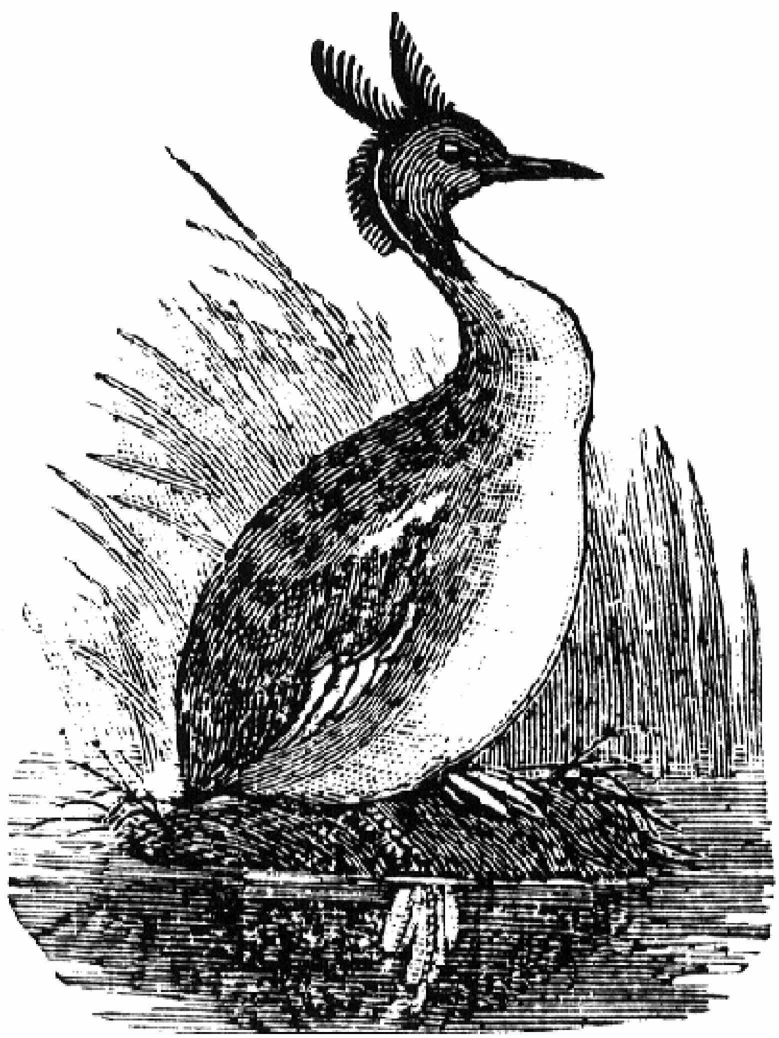


Figure 16.08 Dingus & Rowe

Pathway 3 (Ciconiformes) includes the storks, ibises, shoebills, adjutants, jabiru, condors, and several others (fig. 16.09). The lineage includes approximately 130 species worldwide, and most of its members dine voraciously on small vertebrates, mollusks, insects, crustaceans, and carrion. Flamingos, whose kinship to the rest has been questioned, use specialized bills to filter blue-green algae and diatoms from the water.

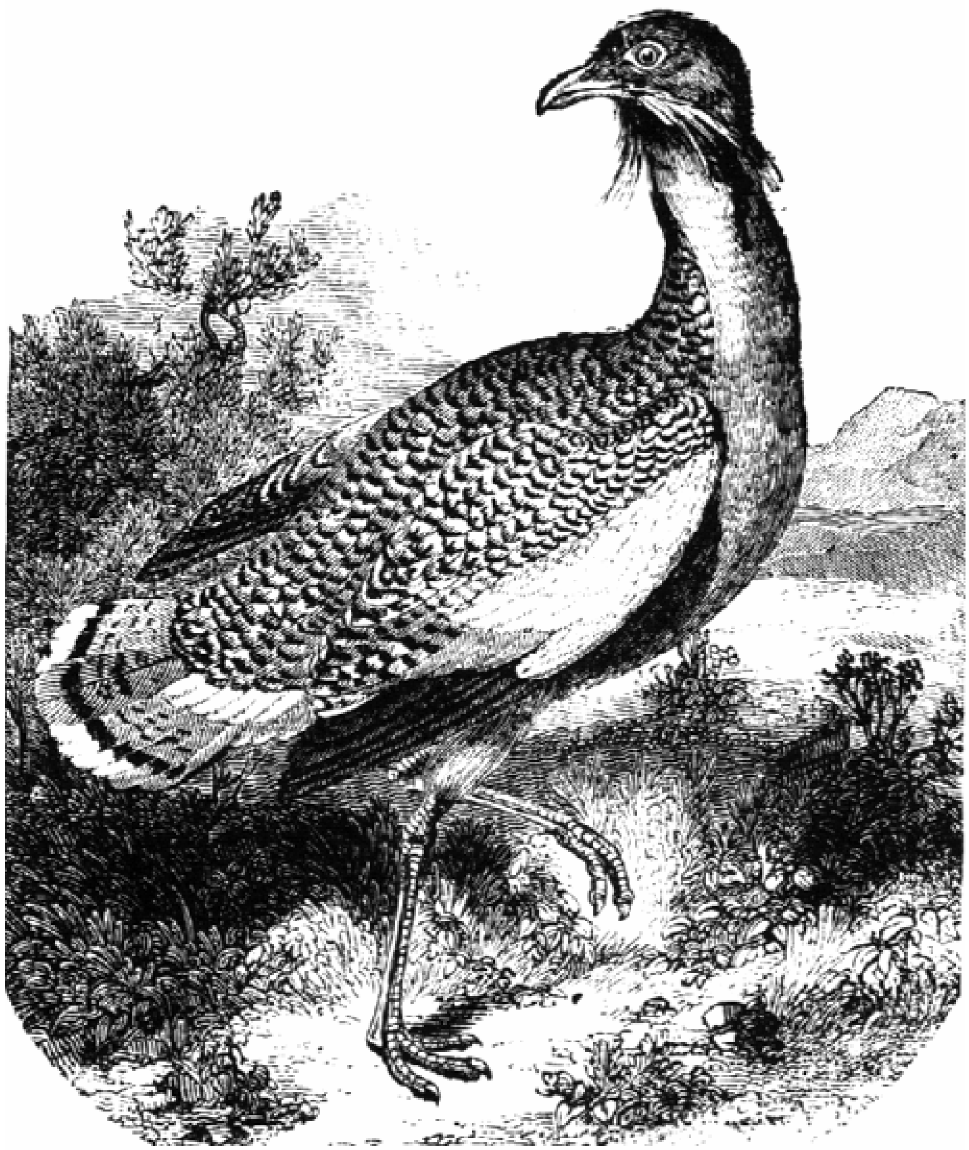


Figure 16.10 Dingus & Rowe

Pathway 4 includes a seemingly eclectic assemblage of pigeons, herons, cranes, and shorebirds, and the interrelationships among these are uncertain. We have already met the shorebirds (Chadriiformes) -- the gulls, auks, and their relatives. The crane lineage (Gruiformes) includes 196 species of predators that stalk shores, shallows, forest floors, and grasslands of the world (fig. 16.10). Larger cranes can soar and undertake long migrations, but several flightless endemic species have evolved on Pacific islands. From Paleocene rocks in South America, we can trace a lineage of predatory birds that ruled the top of the Tertiary food chain (fig. 16.11).

Figure 16.11 Dingus & Rowe

Some could fly, but other giant forms were flightless with reduced wings. One of the largest was *Titanis,* a 10-foot tall form with a huge skull, a long massive beak, and short wings. It originated in South America and migrated overland to North America about 7.5 million years ago, as the two continents drifted together and the isthmus of Panama formed. A second lineage of giant flightless birds--Diatrymidae--is found in early Tertiary rocks of the northern continents (fig. 16.12). *Diatryma* is its best known member, standing over six feet tall and weighing close to 300 pounds. It is generally considered to have been predaceous, but it has recently been depicted in controversial reconstructions as a scavenger or browsing herbivore[11].

Figure 16.12 Dingus & Rowe

Also found along this part of pathway 4 are the rails. Ecologists joke about the "rail rule": seemingly every island in the South Pacific has its own distinct species of rail. Early rails flew from island to island, eventually colonizing nearly all of them. Being naturally weak and reluctant flyers, the colonists on many islands became flightless.

Food and nesting space around the island's shores was in adequate supply, and predatory mammals and reptiles from the mainland were generally lacking. Each colony became isolated from the others and gene flow among them ceased. Archaeological excavations on islands across Pacifica are discovering new species of extinct rails at an astonishing pace[12].

Two more adaptive radiations of woodland birds can be traced along pathway 4. One includes the herons, egrets, and bitterns (Ardeidae), with 65 living species that hunt the woodlands and waterways of the world (fig. 16.13). Among these are several endemic island species. The other woodland radiation (fig. 16.14) includes the 313 living species of pigeons and doves (Columbiformes). Many endemic islands species are found among these as well, including flightless forms like the extinct Dodo. The relationships among all these diverse parts of pathway 4 are unresolved. Most ornithologists agree that the cranes and herons are close cousins, and some believe that storks are related to them as well. Whether the shorebirds are part of this lineage is controversial.

Figure 16.13 Dingus & Rowe

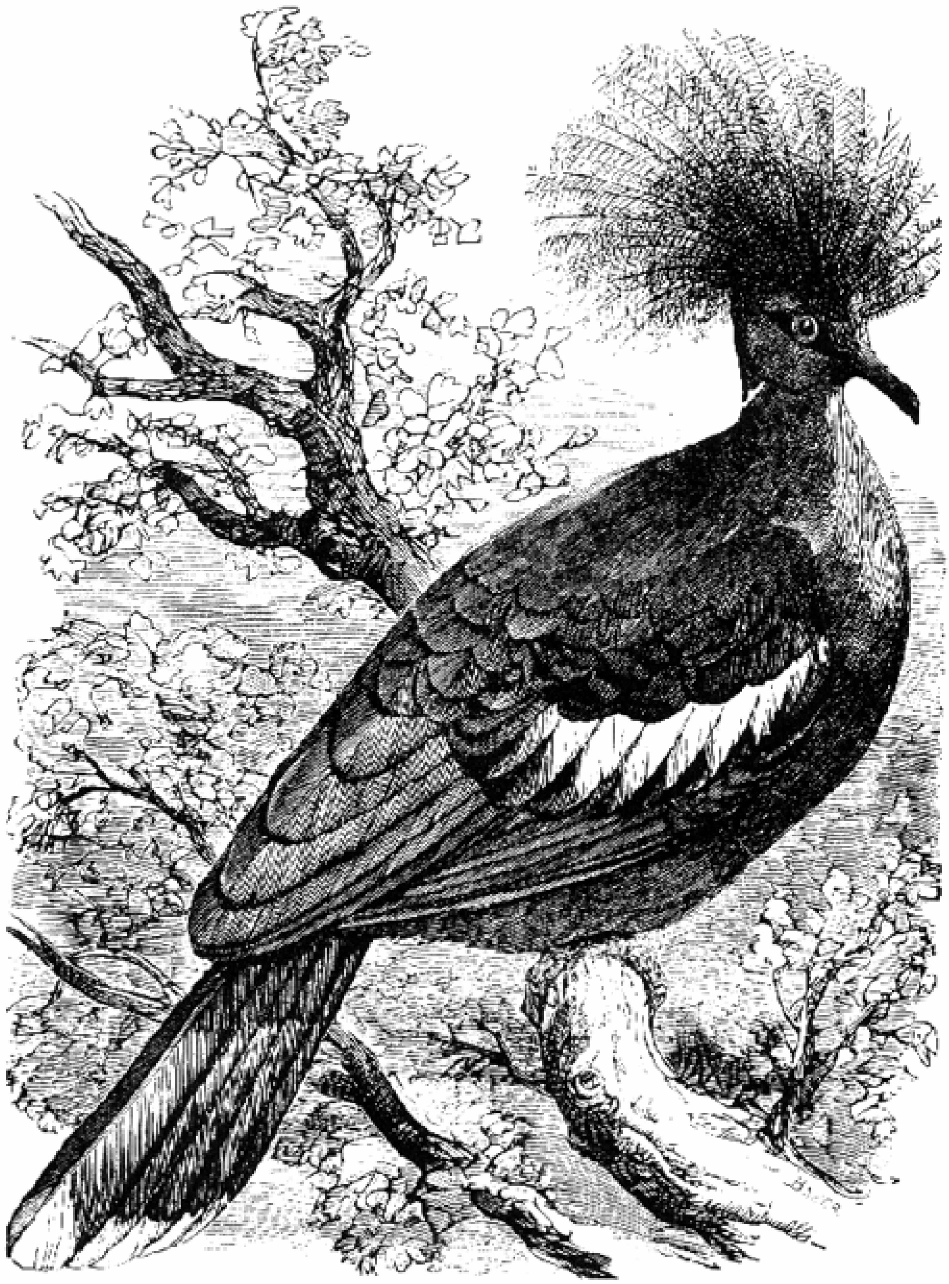


Figure 16.14 Dingus & Rowe

Pathway 5 includes the raptorial owls (Strigiformes) and the eagles, falcons, and ossprey (Falconiformes). They are among today's most consummate hunters, sustaining a theropod tradition of predatory excellence (fig. 16.15). Both lineages have a worldwide distribution that includes endemic island species like the Bare-legged owl of Cuba and the New Guinea Eagle. All have short, hooked beaks and strongly hooked talons, with which they prey on other birds, small vertebrates. Some hawks are excellent runners. Spotting their prey from the air, they land and give chase through the undergrowth and on foot before leaping and grabbing the prey with their talons. Falcons are the fastest dinosaurs, diving at speeds up to 175 miles per hour, typically raking their prey by diving and tumbling it out of the sky. The fossil record for pathway 5 extends back into the early Paleocene.

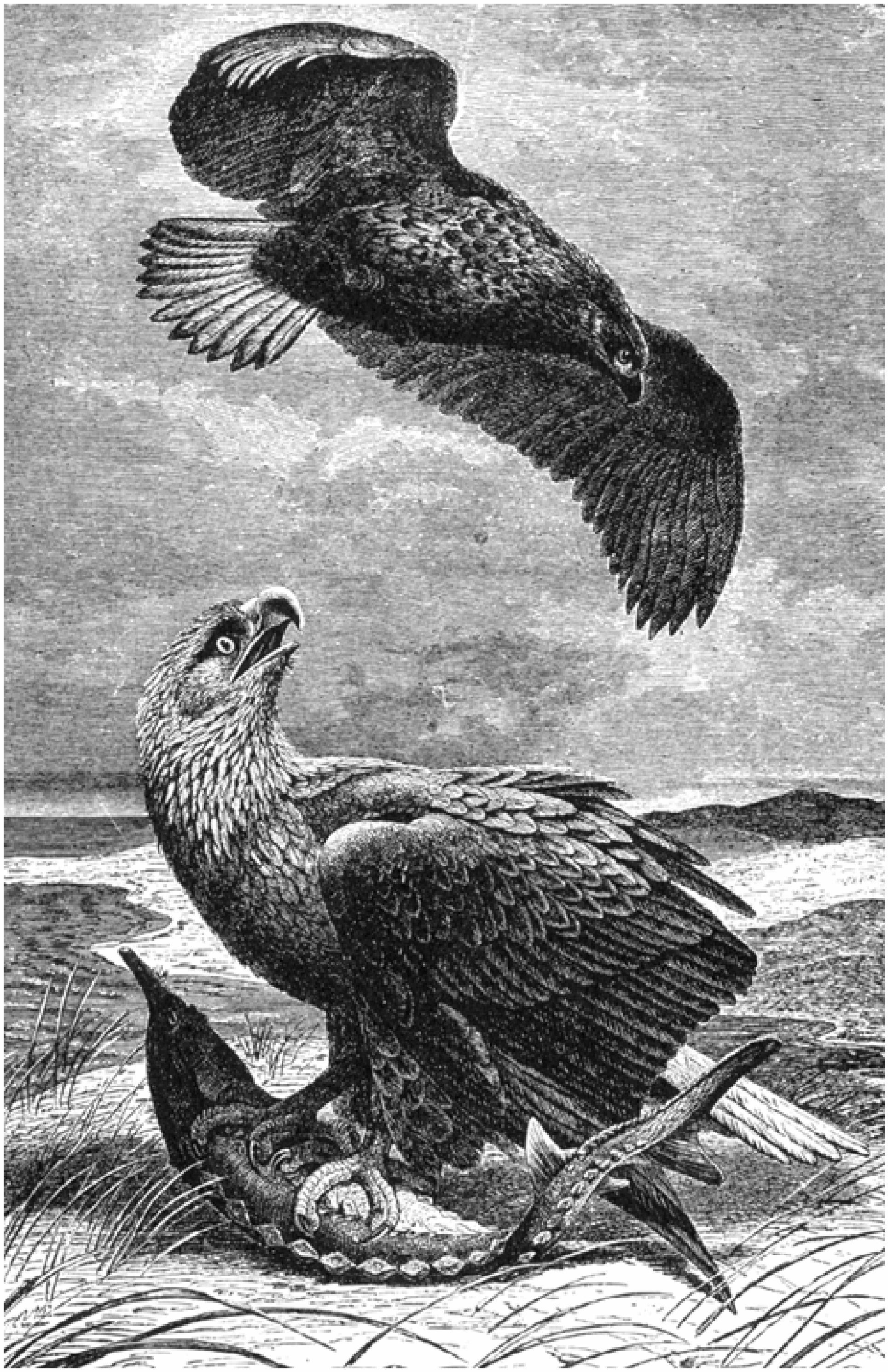


Figure 16.15 Dingus & Rowe

Pathways 6, 7, and 8 include still more woodland bird lineages, who made modest radiations into the woodlands and brushlands of the Old World[13]. These are the touracos and plantain-eaters (Muscophagidae), who live along dense forest edges and in wooded areas near water in sub-Saharan Africa (fig. 16.16). Their fossil record extends back to the Eocene. There are six species of mousebirds (Coliidae), all living around brushlands and forest edges south of the Sahara (fig. 16.17). Mousebirds are good flyers but only over short distances. When foraging for fruit, seeds, and insects, they climb through trees and brush using their feet and bill. Their fossil record also extends back to the Eocene. The last radiation includes 17 species of buttonquail (Tournicidae), which inhabit grasslands and brushlands around the western Mediterranean, much of Africa, southern Asia, Malaysia, Australia, and adjacent islands. Their meager fossil record extends only to the Pliocene, although it must be a far more ancient line.

Figure 16.16 Dingus & Rowe

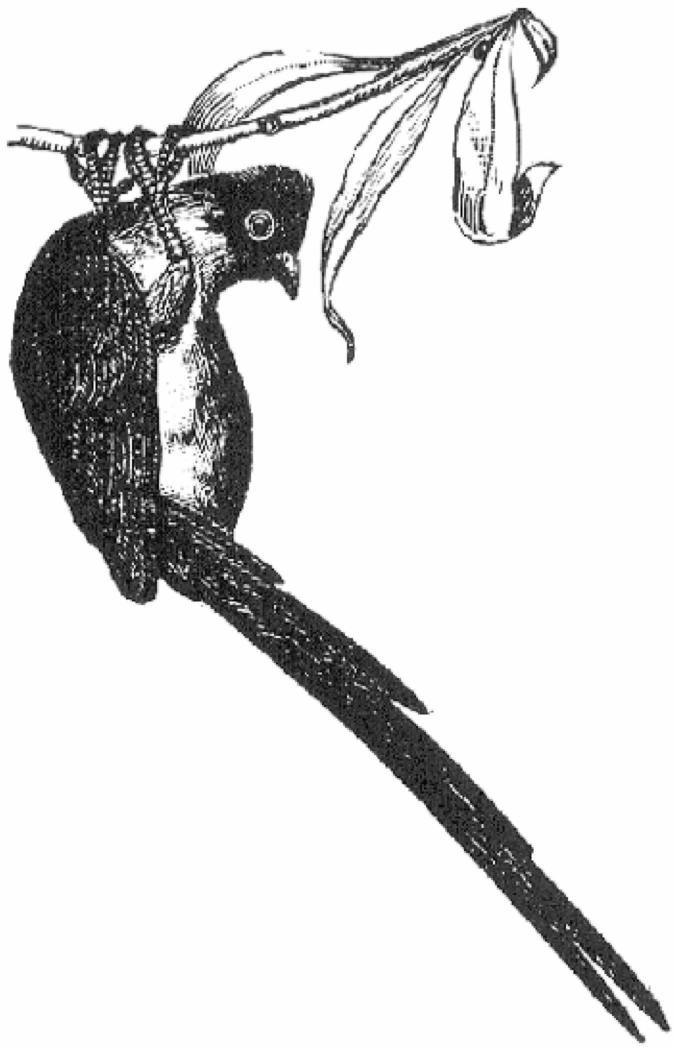


Figure 16.17 Dingus & Rowe

On pathway 9 are the swifts, hummingbirds, and nightjars (Apodiformes), another marvelously diverse lineage of woodland birds (fig. 16.18). There are 103 species of swifts worldwide. Once again we find some species that are wide-ranging, and others that are endemic to South Pacific islands. Swifts have long pointed wings and perform with

Figure 16.18 Dingus & Rowe

great aerial dexterity, capturing all their food--chiefly insects--on the wing. Hummingbirds form a dazzling array of 319 species, most of whom are concentrated in northern South America[14], where they drink nectar and catch insects in the flowers of the forest and brushlands. The Puerto Rican Emerald hummingbird and the Jamaican Streamertail are among several island endemics. The Cuban Bee hummingbird is the smallest known dinosaur, weighing about six grams. Nighthjars, frogmouths, owlet-frogmouths, and potoos comprise 105 species of night birds[15]. They are often allied with owls, but their affinities are highly controversial. Nightjars and nighthawks include both wide-ranging species that inhabit forests and brushlandsand, and endemic island species. Frogmouths and owlet-frogmouths live in brushlands and forests around Australia and the Indian Ocean. The potoos and Oilbird live in central Mexico and South America, in forested or semi-forested regions. The fossil record for this pathway extends back to the Eocene[16].

Figure 16.19 Dingus & Rowe

Pathway 10 includes the parrots (Psittaciformes), which today comprises a spectacular radiation of woodland birds (fig. 16.19). Today there are 358 species of lorys, lorikeets, cockatoos, racquet-tails, rosellas, parakeets, lovebirds, parrots, and macaws inhabiting the forests, savannas, brushlands, and urban areas in tropical and temperate regions around the world[16]. In historic times, parrots ventured up to about 40^{o} N. latitude in North America and 35^{o} N. in Asia[17]. Numerous endemic species are found today on islands in the eastern Pacific and Indian Ocean. Most are strictly arboreal and strong flyers, yet most are non-migratory. They are most diverse in the southern hemisphere, but their fossil record is poor. Island archaeological sites are the richest sources for fossil parrots, where a surprising diversity is now being unearthed.

Pathway 11, the cuckoo lineage (Cuculiformes) comprises several more adaptive radiations that exploited forests, woodlands, brushlands, and deserts. Most of the 143 living species[18]species are predatory, and some are parasitic, laying their eggs in the nests of other birds. Young cuckoos toss the host hatchlings out of the nest and are reared by the host parents, whose own progeny have been killed.

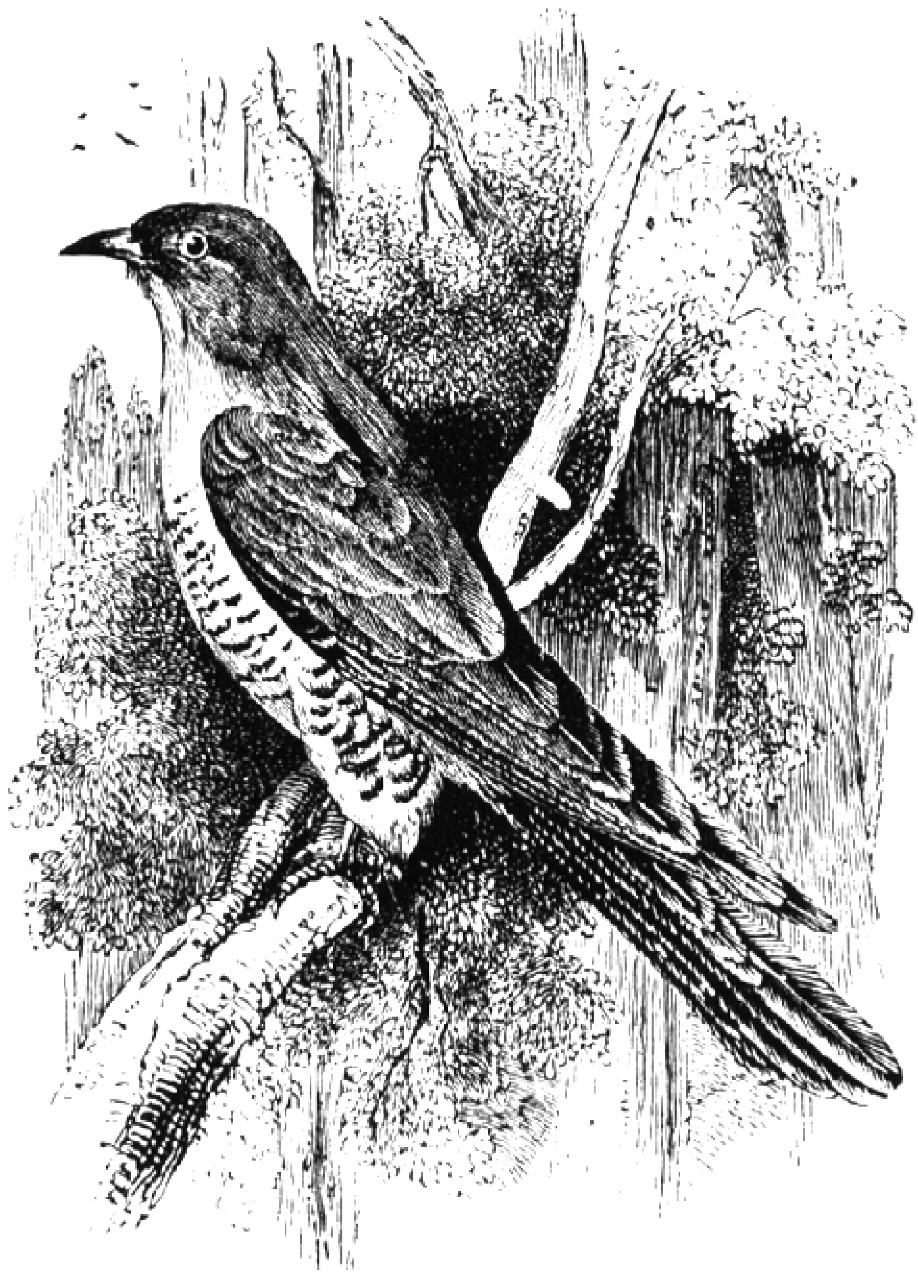


Figure 16.20 Dingus & Rowe

This brings us to pathway 12, the last and largest avian lineage. This huge evolutionary highway connects 6000 living species inhabiting the woodlands and savannas of the world. Most are fearsome predators, although none is large (fig. 16.21). There are three major trails branching from this path and a host of smaller ones. The first

Figure 16.21 Dingus & Rowe

(Coraciformes) includes the kingfishers and relatives[19]. There are 94 living species that populate wooded streams, lakes, marshes, and swamps. Their large heads support a massive bill, and they hunt while perching near or hovering over water to spot their prey, which can be nearly their own body size and still be swallowed. Also included on this trail are 56 living species of hornbills, that range throughout the woodlands of Africa, tropical Asia, Malaysia, and the Philippines. Another coraciform radiation is represented today by 36 species of the trogons, living in humid forests, open woodlands, and mountains of tropical and subtropical regions around the world. Smaller coraciform trails include the bee-eaters, rollers, hoopos, woodhoopoes, and motmots. Pound for pound, the coraciform lineage includes the most fearsome of living theropods.

Figure 16.22 Dingus & Rowe

Next on pathway 12 are the 215 species of woodpeckers and wrynecks (Piciformes), who inhabit woodlands around the world. The toucans lineage includes 56 species that range from Vera Cruz to northern Argentina. They are usually brightly colored omnivores with huge bills that they use to catch small birds, reptiles, mammals, large insects, and to eat fruit. The oldest fossils from along this pathway are Miocene in age, but the lineage is probably much older.

Last, and more diverse than all other birds combined, is Passeriformes. Approximately 5172 species--60% of all living birds--belong to the passeriform lineage[20]. This line exploited to an unprecedented degree the woodlands, deserts, forests, brushlands, savanna, swamps and similar habitats, from the sea to the highest mountains. Anywhere that you can find both open ground and vegetation rising above it, you will a passeriform bird. Some are strong flyers, and some are migratory. They eat insects, spiders, snails, crustaceans, small vertebrates, seeds, fruits, nuts, and other vegetation. The fossil record of Passeriformes extends back only to the Miocene[21]. However, their relationship to other birds projects a ghost lineage at least back into the Eocene, and molecular data projects their lineage as far back as the Cretaceous[22]. Passeriform birds represent by far the most rapid and most diverse adaptive radiation in the entire 300-million-year history of the dinosaur lineage. The remaining lineages are far too numerous to describe in any detail, but simply reading their names (Table 1) conveys a vivid idea of their vast diversity.

Diversity in Decline

Having traced the great post-Cretaceous diversification of dinosaurs, we now return to the issue of dinosaur extinction. First, we need to introduce a geological time period that has never before figured into discussions of dinosaur extinction--the Quaternary. It began about 1.6 million years ago, and extends to the present day. The Quaternary is divided into two epochs. The Pleistocene, which extends from 1.6 MA to about 10,000 ago, includes the great Ice Ages that our 'cave-man' ancestors had to contend with. The Pleistocene was followed by the Holocene, which extends from 10,000 years ago until the present. We live in the Holocene. The great adaptive radiation of birds continued virtually unabated throughout the Tertiary. Although many species arose and died out, the overall trend reflected a global increase in the numbers of species. But from Quaternary sediments, evidence has slowly begun to emerge that this trend has reversed.

An episode of mass extinction on a world-wide scale took place during the Quaternary. Like the K-T extinction, dinosaurs were not the only organisms affected.

Like the K-T extinction debate, several killing mechanisms have been implicated, and the relative influence of each is hotly debated. Thanks to a finely calibrated time scale for the Quaternary, we can tease apart the proposed causes and effects on a finer scale than is possible for the events of 65 million years ago. And the ability to tell time precisely provides evidence of at least three separate pulses of extinction that affected birds during the Quaternary. Some paleontologists argue that there was a single mechanism behind each one, while others argue that the three pulses had more than one cause.

The first pulse occurred during the Pleistocene and it produced a great loss of global diversity. Both climatic change and human activity have been implicated, with some scientists attributing all the losses to one or the other cause, and some to a combination of both. There is little doubt that the Pleistocene was a period of climatic fluctuation, as a succession of Ice Age glacial advances and retreats crossed vast regions[24]. From the north pole southwards, the Pleistocene ice sheets advanced and retreated in five major pulses, blanketing large regions of North America, Europe, and northern Asia. Ice also advanced down from many of the world's major mountain chains, and global cooling affected the Southern Hemisphere almost as severely as the Northern.

Since the Late Pleistocene, the overall climatic trend has been one of increased warming, although minor pulses of cooling also occurred as our modern climate emerged. At the peak of glacial coverage, the mean annual temperature was 5° to 7°C colder than today. About 14,500 years ago the glaciers began to retreat as a global climatic warming trend took effect. There was one last pulse of cold between 10,000 and 11,000 years ago, which marked the end of the Pleistocene epoch and the beginning of the Holocene. Since then, the Earth's climate has become warmer and relatively more stable. By about 4000 years ago, it came to resemble the climate over much of the world today[25].

By the end of the Pleistocene, a momentous loss of diversity had decimated large vertebrates[26]. In North America nearly three-quarters of the larger mammals became extinct, including mammoths, mastodons, saber-toothed cats, horses, tapirs, camels, ground sloths, and the bizarre glyptodonts--giant cousins of the modern armadillo. In South America, a similar proportion of large species became extinct. In Australia, 55 mammalian species are now known to have been lost. Severe losses in Europe claimed the woolly rhino, mammoths, and the giant deer, although many lost European species survived elsewhere in the world, such as the hippo, horse, musk ox, and hyaena.

Some of the largest birds were also affected, including the giant flightless cranes like *Titanis.* They had been the dominant terrestrial predators in South America over most of the Tertiary. Although *Titanus* reached North America in the Pleistocene, it perished before the Holocene began. A Pleistocene condor named *Teratornis*, larger than the California and Andean Condors, also disappeared. Its bones are among the most commonly preserved in the older deposits of the famous Rancho La Brea tar pits, but it evidently died out by the Holocene. A lineage known as the Gallinuloididae, a cousin of modern turkeys, had also died out by the end of the Pleistocene. As many as 28 species of birds may have become extinct at the end of the Pleistocene[27].

One group of paleontologists, led by Paul Martin (University of Arizona), alleges that human overkill was behind the surge of Pleistocene extinctions[28]. Archeological sites have produced the bones of extinct animals in association with human artifacts, along with evidence that people butchered the animals for food. So, there is little doubt that humans preyed on the extinct species. But Martin maintains that the extinction of the mammalian 'megafauna' was a rapid 'blitzkrieg' in which the human invaders into North Americans rapidly fanned out across the continent, from Alaska south and east to the Gulf Coastal Plane, and decimated the large mammals in their path. Owing to economies of scale, early human hunters preferentially hunted the large animals first. If climate had been responsible, they argue, then small mammals and birds should have suffered extinction as well.

Opponents to the human overkill hypothesis have marshaled several arguments exonerating our Pleistocene ancestors in the worst of the losses, They point instead to the climatic fluctuations of the Ice Ages. First, they argue that small vertebrates *were* affected during the Pleistocene, along with the megafauna. Although the losses weren't as great, the geographic ranges of many small vertebrates became more restricted and entire vertebrate communities were reorganized as a result. To better understand the effects of climatic change on late Pleistocene and Holocene mammals, a massive computer database was recently compiled by Ernest Lundelius (University of Texas at Austin), and his former graduate students Russell Graham (Denver Museum of Natural History), and Rickard Toomey and Eric Schroeder (Illinois Natural History Museum), together with more than a dozen colleagues from around the country. The database, known as FAUNMAP[29], contains records for nearly 3000 Quaternary fossil localities in the continental US and Alaska. Each locality represented a collection of fossil and sub-fossil mammals that had been identified and curated in North American natural history museum collections. Each locality's age was determined by radiocarbon methods, whose usefulness is confined to the last 50,000 years. FAUNMAP uses a computer to map the distributions of past faunal and environmental characteristics as they change through time. The database included a wide range of environmental information, such as the extent of the ice sheet at different times and the precise location of each site.

The FAUNMAP analysis revealed a more heterogeneous environment during the early Pleistocene than in later times, in which a higher diversity of mammals existed than at present. During the Holocene warming episode, some mammals dispersed northward, tracking a northward shift in their preferred environment. But different species responded at independent rates and times, moving in different directions. The retreating glaciers left a landscape that was much more uniform in its topography and faunal composition. As Holocene warming progressed, the loss in environmental heterogeneity corresponded with a loss in diversity. The large animals, with slower generation times, were the most severely affected by the loss of environmental heterogeneity. Their decline may have been helped along by people, but climate was probably the major factor.

Other scientists support this conclusion with the argument that global human populations were very small during the Pleistocene, a point that we will return to in a later chapter. The low state of human technology during the Pleistocene is another factor to consider-- humans probably did not have sufficient killing power to have wiped out all the species that went extinct in the Pleistocene. Still other scientists have argued that the timing of events recorded in the archeological record--at least in North America is more complex than claimed by the overkill proponents. The blitzkrieg should have progressed from northeast to southwest, but instead the opposite pattern of loss occurred[30].

In Australia, the situation is also complex, and the solution on this continent may or may not have been the same as in North America. Humans had arrive on that continent by 60,000 years ago. Between 30,000 and 18,000 years ago, a major wave of megafaunal extinction had swept over the continent. Human impacts may have strongest by increasing the frequency of fires. Increased concentrations of charcoal are found in sediments dating back about 30,000 years[31]. Fires altered the vegetation and erosion increased, which further degraded the Australian habitat and accelerated the pace of extinction. But there is also evidence that the Australian climate became more seasonable, with dry intervals, starting about 25,000 years ago[32]. This may have led to a higher frequency of natural fires, and the climatic stress may have had a role in the extinction.

So, even though humans lived during the Pleistocene, their exact role in the Pleistocene losses may have been different in different parts of the world, and climate remains a major suspect.

Evidence being unearthed from islands of the Pacific basin, one of the greatest sources of avian diversity, indicates that there was a second pulse of extinction that followed the great losses of the Pleistocene. Zooarcheological research indicates that the second pulse post-dated the Pleistocene extinction by several thousand years. At the beginning of the Quaternary, for example, there were at least 33 species of ostrich-like ratites. Archaeological records indicate that most Pleistocene ratites survived far into the Holocene, some until only a few hundred years ago. But only eleven species survive today[33]. The same pattern holds for a list of other birds and mammals that is growing, as collaborating zoologists and archaeologists survey Holocene history in detail. Although the climate stabilized around its current patterns during that time, the loss of species didn't stop and in some cases it accelerated. Owing to its timing--several thousand years after the last glacial retreat--this second pulse of extinction is difficult to attribute to climate alone.

Coda

Looking at the history of the entire dinosaur lineage, it is a myth that theropods surrendered their role as top predator at the end of the Cretaceous, at least in some parts of the world. In South America and elsewhere, giant predatory theropod birds dominated terrestrial faunas for millions of years after the K/T boundary. Today, feathered raptors remain at the top of the food chain in many parts of the world, having inherited the role from some of their Mesozoic relatives. In many ways, the post-Cretaceous history of avian dinosaurs is a continuation of what took place in the Mesozoic.

To observe the communities and social interactions among living birds is to see their intelligence and complexity. To encounter birds in nature as they soar, dive, swim, sing, to see them hunt on the ground, in the trees, or under the ice, is to witness more than we can accomplish with our most elaborate machine. How different from its traditional connotation is the phylogenetic image of Dinosauria, with powerful brains, sophisticated 'bio-technology,' and a vast diversity of living species. E. O. Wilson describes that "Great biological diversity takes long stretches of geological time and the accumulation of large reservoirs of unique genes." The evidence described above suggests that the great radiation of birds took about 120 million years - nearly twice the duration of avian history accorded by the Phoenix hypothesis. But like all else in Life, it would not be sustained forever. After a debilitating setback in the Pleistocene, the decline has continued into the Holocene as dinosaur history has become inextricably entangled with our own.

Chapter 16, The Mistaken Extinction, by Lowell Dingus and Timothy Rowe, New York, W. H. Freeman, 1998.

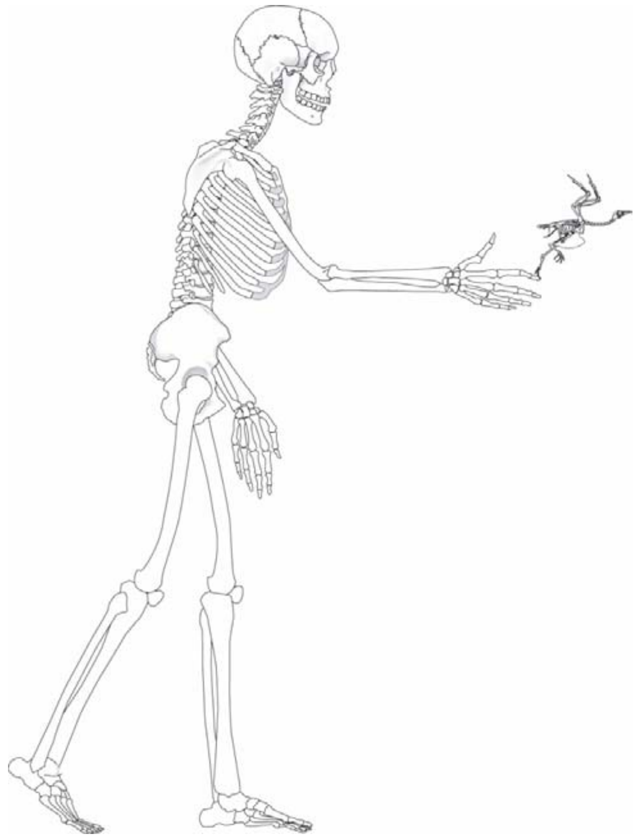


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Table 1

Major Groups of Passeriformes, ordered by number of species (data from the tribes of birds in Sibley, C. G., and B. L. Monroe, Jr., 1990. Distribution and Taxonomy of birds of the World. New Haven, Yale University Press.

Tyrannidae (537 species) Flycatchers, Tityras, Becards, Cotingas, Plantcutters, Sharpbill, Manakins

Funariidae (280 species) Tanagers, Neotropical honeycreepers, Plushcap, Seedeaters, Flower-piercers

Thraupini (413 sp.) Ovenbirds, Woodcreepers

Timaliini (233 species) Babblers

Acrocephalinae (221 species) Leaf-warblers

Thamnophilidae (188 species) Typical antbirds

Emberizini (156 species) Buntings, Longspurs, Towhees

Saxicolini (155 species) Chats

Strildini (140 species) Estrildine finches

Pycnonotidae (137 species) Bulbuls

Carduelini (136 species) Goldfinches, Crossbills

Nectariidae (123 species) Sunbirds, Spiderhunters

Cisticolidae (119 species) African warblers

Corvini (117 species) Crows, Jays, Magpies, Nutcrackers

Ploceinae (117 species) Weavers

Parulini (115 species) Wood warblers

Muscicapini (115 species) Old World flycatchers

Sturnini (114 species) Starlings, Mynas

Oriolini (111 species) Orioles, Cuckooshrikes

Malaconotinae (106 species) Bush-shrikes, Helmet-shrikes, Vangas

Monarchini (98 species) Monarchs, Magpie-larks

Certhiidae (97 species) Creepers

Icterini (97 species) Troupials, Meadowlarks, New World blackbirds

Zosteropidae (96 species) White-eyes

Alaudidae (91 species) Larks

Hirundininae (89 species) Swallows, River-martins

Troglodytinae (75 species) Wrens

Pardalotidae (68 species) Thornbills, Scrubwrens, Bristlebirds, Pardalotes

Motacillinae (65 species) Wagtails, Pipits

Pachycephalinae (59 species) Whistlers, Shrike-thrushes, Shrike-tits, Sittellas

Formicariidae (56 species) Ground antbirds

Garrulacinae (54 species) Laughing thrushes

Parinae (53 species) Titmice, Chickadees

Vireonidae (51 species) Vireos, Peppershrikes

Eopsaltriidae (46 species) Australo-Papuan robins

Paradisaeini (45 species) Birds-of-paradise

Dicaeini (44 species) Flowerpeckers

Rhipidurini (42 species) Fantails

Cardinalini (42 species) Cardinals

Passerinae (36 species) Sparrows

Mimini (34 species) Mockingbirds, Catbirds, Thrashers

Pittidae (31 species) Pittas

Drepanidini (30 species) Hawaiian Honeycreepers

Laniidae (30 species) True Shrikes

Rhinocryptidae (28 species) Tapaculos

Maluridae (26 species) Fairywrens, Grasswrens, Emuwrens

Sittidae (25 species) Nuthatches, Wallcreepers

Artamini (24 species) Currawongs, Woodswallows

Dicrurini (24 species) Drongos

Sylviini (22 species) Sylvia

Megalurinae (21 species) Grass-warblers

Ptilonorhynchidae (20 species) Bowerbirds

Polioptilinae (15 species) Gnatcatchers, Gnatwrens

Cinclosomatinae (15 species) Quail-thrushes, Whipbirds

Viduini (15 species) Whydahs

Eurylaimidae (14 species) Broadbills

Prunellinae (13 species) Accentors, Dunnock

Remizinae (12 species) Penduline-tits

Irenidae (10 species) Fairy-bluebirds, Leafbirds

Melanocharitidae (10 species) Melanocharis, Toxorhamphus, Oedistoma

Conopophagidae (8 species) Gnateaters

Aegithalidae (8 species) Long-tailed tits, Bushtits

Climacteridae (7 species) Australo-Papuan treecreepers

Regulidae (6 species) Kinglets

Pomatostomidae (5 species) Australo-Papuan babblers

Cinclidae (5 species) Dippers

Philepittidae (4 species) Asities

Aegithininae (4 species) Ioras

Acanthisittidae (4 species) New Zealand wrens

Ptilogonatini (4 species) Silky-flycatchers

Fringillini (3 species) Chaffinches, Brambling

Callaeatidae (3 species) New Zealand wattlebirds

Bombycillini (3 species) Waxwings

Corcoracinae (2 species) Apostlebird, Australian chough

Orthonychidae (2 species) Logrunners, Chowchillas

Menurineae (2 species) Lyrebirds

Atrichornithinae (2 species) Scrub-birds

Promeropinae (2 species) Sugarbirds

Chamaeini (1 species) Wrentit

Dulini - (1 species) Palmchat

Figure captions for Chapter 16

Figure 16.01 The islands and archipelagos of the western Pacific Basin were one the most prolific sites for the adaptive radiation of birds over the last 100 million years.

Figure 16.02 Phylogeny of modern birds. All living species belong to either the neognath or the paleognath lineages. Among neognaths there are 12 distinct pathways, but the relationships among these are now well established (based on work by Joel Cracraft).

Figure 16.03 The palaeognathous birds include the ratites, like this Ostrich.

Figure 16.04 The tinamou lineage underwent a radiation that produced more than 40 living species in the woodlands of South America. (From F. B. Gill, 1995. Ornithology. W. H. Freeman & Co., New York).

Figure 16.05 This nearly-extinct Prairie Chicken is a representative of Galliformes, a terrestrial bird lineage with nearly 300 living species and a global distribution.

Figure 16.06 The white Pelican - a member of Pelicaniformes - which includes some of the largest liviing birds.

Figure 16.07 The King penguin - a member of Sphenisciformes. The entire history of the penguin lineage has been played out in the Southern Hemisphere.

Figure 16.08 The Crested Grebe - a member of Podicipediformes.

Figure 16.09 The Wood Ibis a member of Ciconiformes.

Figure 16.10 A Bustard - a member of Gruiformes.

Figure 16.11 The skull of Psilopterus australis, an extinct gruiform bird from the Miocene of South America. These birds were the top predators in south America for much of the Tertiary (Photo courtesy American Museum of Natural History).

Figure 16.12 The skeleton of Diatryma gigantea, a giant extinct gruiform bird from the Eocene of South America. (Photo courtesy American Museum of Natural History).

Figure 16.13 The Little White Egret is a member of Ardeidae.

Figure 16.14 The Crowned Pigeon - a columbiform bird - is part of a global radiation that has left more than 300 living species.

Figure 16.15 Steller's Sea Eagle is a member or Falconiformes, which includes some of today's greatest hunters.

Figure 16.16 The Plantain-eater is a member of Musophagidae, a modest radiation of African woodland birds.

Figure 16.17 The Mousebirds (Colddiidae) represent another modest radiation of African woodland birds.

Figure 16.18 The Coquette Hummingbird is a member of Apodiformes.

Figure 16.19 These Macaws are members of Psittaciformes, which radiated extensively through the tropical and subtropical forests of the world.

Figure 16.20 Cuculiformes, include woodland birds like this cuckoo, and ground birds like the american roadrunners.

Figure 16.21 Pound for pound, Coraciformes birds like this Kingfisher are among the most fearsome living predators.

Figure 16.22 The Ivory-billed Woodpecker, a representative of Piciformes. This species has not been sighted in the wild for more than a decade, and is feared extinct.

Figure 16.23 Nearly 6000 species of living birds are members of Passeriformes, the small perching birds.