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What are the Parrots and Where Did They Come From?

The Evolutionary History of the Parrots

CONTENTS

The Marvelous Diversity of Parrots 3

Reconstructing Evolutionary History 5

Fossils, Bones, and Genes 5

The Evolution of Parrots 8

Parrots' Ancestors and Closest Relatives 8

The Most Primitive Parrot 13

The Most Basal Clade of Parrots 15

Other Major Groups of Parrots 16

Box 1. Ancient DNA Reveals the Evolutionary Relationships of the Carolina Parakeet 19

How and When the Parrots Diversified 25

Some Parrot Enigmas 29

What Is a Budgerigar? 29

How Have Different Body Shapes Evolved in the Parrots? 32

THE MARVELOUS DIVERSITY OF PARROTS

The parrots are one of the most marvelously diverse groups of birds in the world. They dazzle the beholder with every color in the rainbow (figure 3). They range in size from tiny pygmy parrots weighing just over 10 grams to giant macaws weighing over a kilogram. They consume a wide variety of foods, including fruit, seeds, nectar, insects, and in a few cases, flesh. They produce large repertoires of sounds, ranging from grating squawks to cheery whistles to, more rarely, long melodious songs. They inhabit a broad array of habitats, from lowland tropical rainforest to high-altitude tundra to desert scrubland to urban jungle. They range over every continent but Antarctica, and inhabit some of the most far-flung islands on the planet. They include some of the most endangered species on Earth and some of the most rapidly expanding and aggressive invaders of human-altered landscapes. Increasingly, research into the lives of wild parrots is revealing that they exhibit a corresponding variety of mating systems, communication signals, social organizations, mental capacities, and life spans. In a great many respects the 360 or so species of parrots represent a textbook

FIGURE 3 Scarlet Macaws, *Ara macao,* playing in a guanacaste tree (*Enterolobium cyclocarpum*) in Costa Rica.

illustration of how the process of evolution can, over much time, lead to the diversification of many species from a single ancestral population.

At the same time, parrots are one of the most physically homogeneous groups of birds. Anyone with a passing familiarity with birds can instantly recognize a parrot by its sharply curved upper beak topped by a fleshy cere, muscular prehensile tongue, relatively big head and stout body, and distinctive zygodactyl feet with two toes pointing forward and two pointing back (figure 4). This combination of anatomical features clearly sets parrots apart from other birds. There are other, less obvious, commonalities in physiology, behavior, and ecology that tend to distinguish parrots from most other birds. These shared features illustrate another principal feature of evolution: that it tinkers with the materials at hand rather than starting anew with each species. In other words, major innovations are rare. What more typically happens is that features already present in an ancestor are slowly modified through natural selection over many generations to produce a constrained range of variations on the basic template as different lineages adapt to changing and localized environments.

In the following chapters we will delve deep into what recent scientific investigations have revealed about the lives of wild parrots. We will discuss how parrots perceive the world around them, how individuals go about their daily lives and interact with others, and how populations are adapting to a world that is rapidly changing. Our focus will be both on what

FIGURE 4 Nestlings of the Blue-fronted Amazon, *Amazona aestiva,* illustrating some of the basic morphological features shared by all parrots.

these investigations tell us about parrots in general, and on what can be learned from the interesting exceptions to these generalities. But before we start this exploration, we want to set the stage by summarizing the current state of knowledge of the evolutionary history of parrots: Where did they come from, how did they diversify, who among them is most closely related to whom, and what does this evolutionary history reveal about the process of evolution itself? To understand these topics, we must first understand how scientists explore what happened in the long-distant past.

RECONSTRUCTING EVOLUTIONARY HISTORY

Fossils, Bones, and Genes

Reconstructing the past history of life is both a historical exercise and a scientific one. Scientists typically illustrate evolutionary patterns as trees, with the common ancestor of a group of species placed at the root, and existing species at the tips of the branches. The branching points between the root and the tips represent points where a single lineage split to produce two new lineages, while the length of each branch represents the amount of time or evolutionary change between branching points. As an aside, this representation of

evolutionary history in tree form was an innovation of Charles Darwin himself, appearing first in his scientific notebook and then popularized in his seminal work, *On the Origin of Species*. These trees, or *phylogenies*, as they are termed by evolutionary biologists, are best viewed as hypotheses of how evolution occurred in a particular group of species. As such, they represent a well-informed supposition as to who is more closely related to whom, and when and how current species diversified from a common ancestor. As we will see below, such phylogenies also furnish predictions as to what traits or attributes might be shared among which species. Like all scientific hypotheses, they are subject to a rigorous process involving the collection and analysis of data and a careful evaluation of whether these results support or contradict the particular hypothesis in question. If the data are consistent with the hypothesis, then it remains standing as our best estimate of how evolution proceeded, for now. But, like all hypotheses, it is always subject to further testing and investigation with new data, and such investigations may well lead to modifications of the hypothesis and a new understanding of the past.

What sort of data do evolutionary biologists use to reconstruct evolutionary history? There are three primary sources: fossils of ancient taxa, physical traits measured from the anatomy of current specimens, and genetic data sampled from living or preserved animals. Fossils have the great virtue of concretely demonstrating how specific lineages appeared in the past, including lineages that have become extinct. Importantly, the geologic layer in which fossils are found provides context and can pinpoint when and where the lineage with this trait existed. Such data can be invaluable for calibrating the timing of branching points in a tree and grounding the hypotheses of how evolution proceeded in a group. The downside to fossils is that they can be hard to find and are typically fragmentary in nature, and thus provide only a partial view of the evolutionary past of an entire group of species. As we will see below, such is the case with the parrots.

In addition to fossils, scientists can use data from species still in existence and look for patterns of shared similarities and differences. These data can then be used to reconstruct a phylogeny that best explains the patterns of shared similarities. In the past these trees were often based on the straightforward principle of parsimony, which assumes that trees that require the fewest evolutionary changes are more likely than those that require more changes; now more mathematically sophisticated approaches are employed.

Scientists prefer to build such trees using traits that are easily and reliably measured. The reason for this is simple: Even a few species can be arranged into enormous number of alternative trees with different branching patterns, each one representing a different hypothetical evolutionary history. Distinguishing between these alternate branching patterns is best done with measurements of lots and lots of traits (also called *characters*). More characters generally leads to better discrimination of the small set of trees that fit the data well from among the enormous forest of possible trees that could be constructed for a given set of species. Making these distinctions is a job best left to powerful computers applying carefully developed algorithms; with large numbers of species it can still take these computers weeks to sort through all the billions of possible alternative trees. It is still up to the

scientists, however, to choose and measure their characters carefully so that the trees generated are most likely to represent sound hypotheses of evolutionary history.

Historically, the most abundant characters available to scientists were those provided by gross anatomy and morphology. Museum collections have thousands of specimens that are used for just this purpose, and they are carefully curated in impressive collections of study skins, skeletons, whole bodies in alcohol, and even nests and eggs. These specimens can then be used to painstakingly measure obscure details of the size and arrangement of bones and organs and compare these characters within and among different species. Such careful work exemplifies the classical approach to systematics, the branch of science that aims to reconstruct the evolutionary history of all organisms or, as it is colorfully known, the Tree of Life. Such knowledge was hard-won, however, as even the most creative and careful scientist eventually ran into limits as to how many morphological characters they could reliably measure across an entire set of specimens. This problem was especially acute when trying to compare across very distant branches of the Tree of Life separated by long periods of time from their common ancestor. (Imagine how few characters could be reliably measured across jellyfish, honeybees, and sharks, three distantly related members of the kingdom Animalia.) At the other end of the spectrum, early systematists also had difficulty with homogeneous groups in which many members shared similar values for most morphological traits, leaving few characters that actually helped distinguish among different groups. Such was the problem with the parrots, as their conserved morphology provided few external or even internal characters that varied enough to be useful in building well-resolved evolutionary trees. It took a landmark scientific discovery to break this impasse and eventually provide new insights into the evolutionary history of parrots and the entire Tree of Life.

This breakthrough was the discovery of DNA and the rapid rise of modern molecular genetics it permitted. In 1953, James Watson and Francis Crick, along with Rosalind Franklin and others, described the double-stranded helical structure of a molecule called deoxyribonucleic acid (DNA for short) and proposed that it encoded the genetic information necessary for life. This landmark discovery led to an explosion of studies into how these encoded instructions were used to build organisms, and how these instructions changed as they were passed from one generation to the next. This understanding of the basic molecular mechanisms of inheritance has benefited virtually every field of biology and opened vast new fields of study. The beneficiaries have included systematists, who were quick to realize the insights that direct study of genes themselves could contribute to reconstructing the evolutionary past.

Among the first pioneers of this new field of molecular systematics were Charles Sibley and Jon Ahlquist, who worked together through the late 1970s and 1980s to apply genetic approaches to understanding the evolutionary history of birds (class Aves). Their work culminated in 1990 with the publication of their monumental *Phylogeny and Classification of Birds,* the first large-scale study to apply DNA evidence to avian relationships. There was, however, considerable debate among ornithologists regarding their general approach, which

relied on large-scale comparisons of overall DNA similarity across the entire genomes of pairs of species, and about many of their specific findings that resulted from this DNA–DNA hybridization technique.

Nonetheless, Sibley and Ahlquist's groundbreaking study did spur others to follow in their footsteps, and it revitalized interest in the relationships among major groups of birds. This interest was facilitated by rapid advances in biotechnology that started in the 1980s such as the invention of the polymerase chain reaction (PCR) and the mechanization of DNA sequencing. These technologies allowed researchers to isolate a single stretch of DNA from a sample, amplify many thousands of copies of it, and then read out the sequence of nucleotide base pairs. This DNA sequence could then be compared between species to look for patterns of similarities and differences. With the help of ever-improving computers, these patterns of sharing could then be transformed into trees of evolutionary relationships using many of the same approaches developed for morphological traits. The main benefit for molecular systematists was that they could now compile information from hundreds or thousands of DNA characters, whereas they used to struggle to find a few dozen characters from painstaking examination of morphology. These new biotechnological approaches have led systematists into a golden age of studies aimed at uncovering the evolutionary past of birds and other organisms. It is a golden age that continues today and will no doubt stretch on until such time as a comprehensive and well-supported hypothesis for the entire Tree of Life is produced. And, importantly for us, it has cast new light into the previously obscure history of the parrots.

THE EVOLUTION OF PARROTS

Parrots' Ancestors and Closest Relatives

The origin of parrots themselves is an evolutionary enigma. The unique set of morphological features shared by all parrots sets them well apart from other groups of birds and has made determining the identity of their closest relatives a challenge. In the absence of series of well-defined characteristics shared with another group, avian systematists resorted to proposing a long list of possible candidates as relatives, usually on the basis of a single feature that each shared with the parrots. Various proposed relatives included the pigeons, based on similarities of the humerus bone in the wings; the owls, based on the shared presence of a fleshy cere over a curved bill and features of the skull; the woodpeckers and their relatives, based on the shared presence of zygodactyl feet; the cuckoos and relatives for the same reason; the falcons or the owls, based on the hooked bill; and the toucans, based on the sharing of powder down. Others have noted morphological similarities with the mousebirds, an obscure group of small African birds composed of only six extant species that are able to switch their toes between the zygodactyl formation and the anisodactyl formation, in which three toes point forward and one backward. Most dismissed the shared

presence of curved bills in the falcons and the parrots as a sign of a close relationship, instead explaining it as an example of convergent evolution, in which similar selection pressures lead to the evolution of similar features in distantly related groups. Others pointed out that the same argument could be applied to any of the similarities noted between parrots and other groups of birds. Clearly, morphology was providing little resolution to this thorny question.

The first attempts to answer this question using modern molecular genetics were only somewhat more successful. The comprehensive phylogeny produced by Sibley and Ahlquist using DNA–DNA hybridization suggested that parrots were most closely related to the cuckoos and to a group composed of the swifts and hummingbirds. The actual number of DNA comparisons on which this conclusion was based was limited, however, and the relationships were generally considered provisional until such time as better data were available.

The question of which group of birds is most closely related to parrots was wrapped up in a larger question of how and when the major groups of birds had diverged from their common dinosaur ancestor. This was a big question for scientists, and one that many groups tackled as more genetic tools became available. These new approaches did provide clear answers to some parts of this bigger question. Numerous molecular studies agreed in finding a deep division between the Paleoagnathae, a group composed of the flightless tinamous and ratites (ostriches, emus, and rheas), and all other living birds, the Neoagnathae. Within the Neognathae there was also a clear division between a group called the Galloanserae, consisting of waterfowl and the chicken-like birds, and the Neoaves, a large group containing all other living birds and some 95 percent of avian diversity. It was relationships within this latter group, the Neoaves, that proved the toughest nut to crack.

Distressingly, for over a decade the question of who was related to whom within the Neoaves became less rather than more clear. Study after study proposed different relationships among the major branches of Neoaves, and postulated different closest relatives for the parrots. Why were there such discrepancies among these studies? Part of the issue lay with the use in different studies of different types of genetic markers, which evolve at a distinct rates and may be subject to various evolutionary constraints. Part of it was due to different samples of species and groups from study to study; if a group is present in one study but absent in another it is difficult to reconcile the resulting trees. But part of the disagreement was certainly due to the nature of the problem itself. All these studies did agree on one conclusion: that the diversification of the Neoaves happened in a relatively short period of time, perhaps around the end of the Cretaceous period and the beginning of the Paleogene period, some 65 million years ago (the Paleogene was formerly known as the Lower Tertiary Period, and the boundary between the Cretaceous and Tertiary as the K/T boundary). This was a time of great upheaval in the Earth's biological history, when nearly 50 percent of the world's species became extinct, including the dinosaurs. With such losses came great opportunities for the survivors, as many ecological niches became available to those who could rapidly evolve abilities to exploit them. The result was a period of rapid evolution and diversification

for the birds and other lineages, including the mammals. Such *explosive radiations*, as they are termed, pose a particular challenge for molecular systematists. This is because the rapid splitting of several lineages from a common ancestor leaves little time for the genetic changes used to measure differences between lineages to accumulate along the short branches that connect one separation into separate lineages and the next. As more evidence accumulated, some even suggested that the problem was insoluble—that the divisions between the groups of Neoaves occurred so rapidly that rather than an elegant branching tree, the history of Neoaves should be represented by a squat bush, or comb, with many branches arising simultaneously from the base.

Happily, not all scientists took such a nihilistic view of the effort to resolve relationships among the groups (or *clades*) within Neoaves. In particular, a group of scientists from a number of institutions including the Smithsonian Museum of Natural History, the Field Museum of Natural History, the University of Florida, and Louisiana State Museum coordinated their efforts to sample a large number of genes from the same samples representing all major groups within Neoaves. This large-scale effort culminated in the publication in 2008 of a paper by Shannon Hackett and colleagues in the prestigious journal *Science* that represented the most comprehensive molecular study of birds to date, with 169 species sequenced at 19 different genes. This landmark achievement not only yielded a much clearer family tree for the Neoaves, but it also provided a surprising answer to the question of who was most closely related to the parrots. The authors' various analyses gave strong, if not unanimous, support to a novel grouping of the parrots with the passerines, a group also known as the songbirds. Working backwards in the tree, the next group to have split off was the falcons. In other words, a common ancestor gave rise to the falcons as well as a lineage that later split into the parrots and the passerines, making these latter two groups each other's closest relative (figure 5).

To say that this relationship between the passerines and the parrots was surprising to many would be an understatement. The songbirds had never before appeared on the long list of possible relatives of the parrots in studies based either on morphology or genes. There is an adage in science, made popular by Carl Sagan, that "extraordinary claims require extraordinary evidence." Here was certainly an extraordinary claim, at least for those interested in avian evolution. But was the evidence also extraordinary? Most ornithologists outside those involved in the study viewed it as solid, but perhaps not extraordinary. Many reserved judgment until such time as more evidence was available. They didn't have long to wait. In 2011 Alexandar Suh and colleagues in Germany published a study examining Neoaves relationships using retroposons, an entirely different type of genetic marker whose presence or absence in different lineages was thought to be an especially reliable indicator of shared ancestry. This new study provided further confirmation of a sister relationship between parrots and passerines, with the falcons again appearing as the closest relatives to this group. Further support was provided in 2012 by a study by Ning Wang and colleagues at the University of Florida that utilized a new dataset of thirty genes to explicitly test various hypotheses for the identity of the closest relative of the songbirds. Once again they found

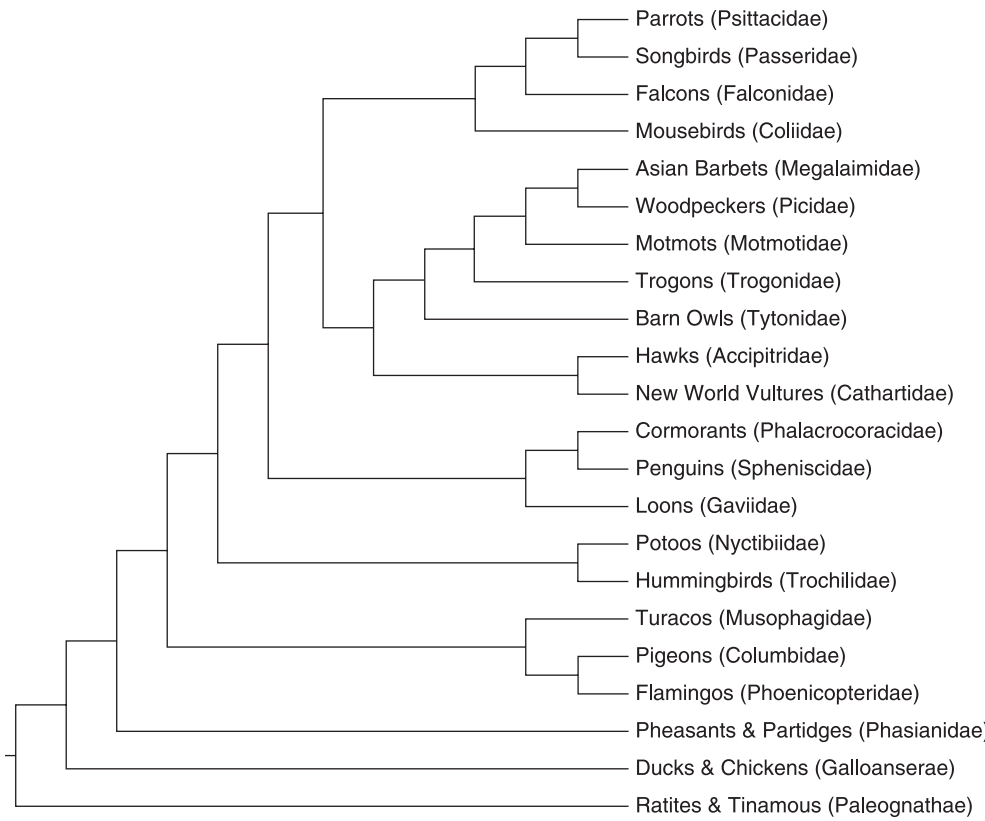


FIGURE 5 Phylogenetic tree illustrating the relationships among some families of Neoaves (the modern birds), including the close relationship between songbirds, parrots, and falcons.

strong evidence in support of a grouping of the parrots and passerines. What was once extraordinary now was looking more like reality.

As I write this chapter,[1] the latest word in this debate is a work by John McCormack and others at a consortium of institutions led by Louisiana State University. They used sequence data from an astounding 1,541 independent genetic loci sampled from representatives of 32 clades within the Neoaves. This work, published in early 2013, used the largest dataset to date, and provided increased resolution for the explosive radiation of Neoaves at the end of the Cretaceous. It provided further support for the sister relationship between parrots and songbirds, with falcons as sister to this group. In just five short years the sister relationship between parrots and songbirds went from one viewed with wide skepticism to one that is emerging as rather solid. All the scientists involved are quick to point out that many uncertainties remain concerning the branching order of these avian groups that diversified so rapidly some 65 million years ago. They continue to collect more and more genetic data using

1. In this chapter the narrator is Tim Wright; in the rest of the chapters it is Cathy Toft.

FIGURE 6 Representatives of the parrots (left: Derbyan Parakeet, *Psittacula derbiana*) and the songbirds (right: Yellow-headed Blackbird, *Xanthocephalus xanthocephalus*). Based on DNA evidence, the parrots and the songbirds are now thought to be each other's closest relatives.

the new techniques from the toolbox of genomics to gain further resolution on this problem. At present, however, there is a growing consensus that the closest relatives to the parrots are indeed the songbirds.

One reason many scientists have had difficulty accepting a sister relationship between parrots and songbirds is that they do not look very much alike (figure 6). Both groups show a great deal of diversity in size, plumage, behavior, and ecological habitats, with the 5,000-plus members of the order Passeriformes showing an even greater diversity in most of these areas than the 360-odd members of the order Psittaciformes. (Recall that in the classical Linnaean hierarchy, species are grouped into genera, which are then grouped into families, which are then grouped into orders, classes, phyla, and kingdoms. The parrots and cockatoos constitute the order Psittaciformes within class Aves, phylum Chordata, and kingdom Animalia.) But in those areas where there is greatest consistency within each group, namely in the shape of the bill and the feet, the passerines and the parrots couldn't be more different. Virtually all the passerines have straight bills, slender legs, and anisodactyl feet, with three toes pointed forward and one pointing back. All the parrots have strongly curved bills, robust legs, and zygodactyl feet, with two toes pointing forward and two pointing back. The sharply different defining traits of these two groups had long obscured what now appears to be the true evolutionary relationship between them. This new finding has prompted the

reexamination of fossil data by paleontologists in search of similarities between the ancestors of these lineages. As we will see in the next section, these paleontologists have found some evidence that ancient ancestors in each group differed from their modern descendants in some of these key features. While the picture is still unclear, it does suggest that the distinct differences between passerines and parrots in bills and feet may not always have been so clear-cut as they are today.

There is, however, one trait of special significance that is shared by parrots and at least some members of the passerines: vocal learning. Both parrots and songbirds are well known for their capacity to acquire vocalizations through vocal learning (see chapter 4). Evolutionary biologists had long inferred that this advanced behavior and the specialized neural pathways underlying it had evolved independently in the songbirds, the parrots, and a third group with vocal learning, the hummingbirds. The newly discovered relationship between songbirds and parrots is forcing a reevaluation of this assumption, and casting new light on studies that examine the neural basis of vocal learning in these three groups.

The studies of higher-order relationships among birds have enmeshed parrots in another debate: Exactly when and where did the parrots diversify? This is a topic we will take up below. But first we want to address another fundamental question: What did the ancestral parrot look like when it first branched off from its closest relative?

The Most Primitive Parrot

The ongoing debate about which group of birds is most closely related to the parrots has cast a new light on a related question, namely the identity and appearance of that most mysterious and ancient of all parrots, the ancestor that gave rise to all subsequent species. The question of the most primitive parrot is one that can be answered in a couple of ways. One method by which scientists sometimes infer the appearance of the "common ancestor" of a group of species is to focus on the first branching point in the evolutionary history of a group and examine any species that descend directly from that ancestor without further diversification. Such species located on long branches from the common ancestor are sometimes considered the most *primitive* species in the larger group, although this term is somewhat of a misnomer. It is based on the assumption that such an early-splitting clade group would more closely resemble the ancestor of that group than any of the other species. A brief inspection of any phylogenetic tree, however, would quickly reveal that all of the existing species (those found on the tips of the tree) would have had roughly the same amount of time to evolve differences from their common ancestor at the root of the tree. In some rare cases, such as the coelacanth fishes that are most basal group of tetrapods, such groups do seem to represent "living fossils" that retain many of the features found in their long-distant ancestors. Generally speaking, though, any one individual modern species does not necessarily provide any more information about the appearance of the common ancestor than any other within the clade.

A second approach that is on firmer logical ground is one called *ancestral state reconstruction*. This approach makes use of clever statistical algorithms to "reconstruct" the appearance

of the common ancestor by taking into account the traits of all extant species and minimizing the amount of change in traits from the common ancestor to the present-day descendants. This approach, although often informative, can be led astray by extinctions of whole lineages, which can radically alter the perception of the characteristics of the larger group by their absence. As we will see below, such appears to be the case with the parrots.

A third, and more robust, way in which scientists try to establish the identity and appearance of the common ancestor of an entire group is through the fossil record. Paleontology, the study of the fossil record, is not without its challenges. Primary among these is the fact that the conditions for the process of fossilization and clear preservation of past life are somewhat rare, particularly for birds. This leads to gaps in the fossil record into which our knowledge must be interpolated. But as paleontologists continue their efforts to find and interpret fossils and systematically target gaps in the record, our knowledge of past life via the fossil record has become more and more comprehensive. Sometimes it provides surprising new insights into evolutionary history.

Given the general homogeneity in morphology of the parrots we see today, it is a reasonable supposition that the ancestral parrot also had the curved beak and other conserved features that characterize all modern parrots. Work by Gerald Mayr of the Frankfurt Natural History Museum, however, suggests that the ancestral parrot looked somewhat different from those of today. He and others have identified a series of fossils from European deposits laid down in the Eocene (35–55 million years ago) that form several distinct clades that have been given such names as Quercypsittacidae and Pseudasturidae. These now-extinct "stem" groups of parrots can be grouped with a modern "crown" group of parrots based on a number of shared similarities in the shape and proportions of their bones, particularly those that make up the zygodactyl foot shared by all these groups. Surprisingly, though, these extinct stem parrots all lack one of the most characteristic features of modern parrots, namely the long and deep upper bill, or maxilla, that curves strongly over a shorter lower bill, or mandible. Mayr has suggested that the curved bill so ubiquitous among modern parrots evolved as an adaptation for eating the larger fruits and nuts that gradually evolved during the early Cenozoic period, which started about 65 million years ago. That is, the diversification of these new food resources provided a driver for natural selection to promote the evolution and subsequent diversification of this new modern model of parrots with curved rather than straight bills. When and where this diversification took place is matter of continued debate that we will turn to below. Intriguingly, these stem parrot fossils are found exclusively in Europe, a region that now hosts parrots only as occasional, human-assisted invaders. It is worth noting that this is only one of several possible evolutionary scenarios; it is also possible that the curved bill found in both parrots and falcons was found in their common ancestor and then secondarily lost in the branch of the parrot family tree that settled in Europe in the Eocene. The discovery of further parrot fossils would surely help distinguish among these competing scenarios. But both the geography and the appearance of these fossils suggest that the evolutionary history of parrots is more dynamic than might be suggested from an examination of the modern parrots alone. As Mayr has aptly put it in a 2014

paper in the journal *Palaeontology*, "the benefits of a complimentary consideration of fossil taxa and molecular phylogenies are mutual," each providing context and insight for new discoveries of the other.

The Most Basal Clade of Parrots

Now that we have a clearer idea of how parrots are thought to appear at their origins, we can turn our attention to understanding relationships among existing groups of parrots. We will start our survey of these relationships at the base of the modern parrot family tree. The term favored by systematists for the clade that split off first from the common ancestor of an entire extant group is *basal clade*, meaning it split off at the base of the phylogenetic tree. So what is the most basal clade within the parrots?

For over two centuries, classical systematists have debated this fundamental question as they wrestled with the difficult task of sorting out relationships among the physically homogeneous parrots. This debate started with the naturalist Comte de Buffon in 1779, continued with work by Count Tommaso Salvadori (so many counts!) in the late 1800s, and stretched through the 1900s with many important contributions, perhaps the most notable being the first appearance of Joseph Forshaw's *Parrots of the World* in 1973. Throughout this long-running debate, there has been much arranging and rearranging of the parrot family tree. This work culminated in an exhaustive 1975 compendium by George Smith of characters measured from bones, muscles, organs, plumage, ecology, and behavior. As a whole, this work led to a fairly consistent view of relationships at the tips of the parrot tree (how species were grouped into genera and genera into tribes), but little consensus on the higher-order relationships that grouped tribes and families within the order Psittaciformes that encompasses all parrots. There was a general view that the cockatoos were the most basal clade in the parrot family tree given their unique combination of features, including an erectile crest, a gall bladder, powder down, and an absence of the Dyck texture in the feather barbs that produces the stunning colors seen in other parrots (see chapter 3). But even Smith, who had compiled the most extensive dataset of his time, was circumspect in his arrangement of relationships and included several other tribes with the cockatoos in a group he placed at the base of the tree. Further resolution of this thorny issue had to wait for the advent of phylogenies based on molecular genetic characters.

Starting in the 1990s and on into the mid-2000s a raft of molecular phylogenies appeared that have vastly improved our understanding of the evolutionary history of parrots. These include studies by Leslie Christidis, Richard Schodde and colleagues, Cristina Miyaki and her students at the Universidade de São Paulo in Brazil, Rolf and Siwo de Kloet at the biotechnology firm Animal Genetics in Florida, Masayoshi Tokita and colleagues at Kyoto University in Japan, Nicole White and colleagues at Murdoch University in Australia, Miguel Schweizer and colleagues at the Naturhistorisches Museum Bern in Switzerland, and an international collaboration led by my own lab at New Mexico State University. These phylogenies all differ slightly in scientific and geographic focus, or in the species sampled and in the genes used to reconstruct a phylogeny. But when viewed together now they provide a much clearer and relatively

consistent view of parrot evolution than that historically afforded by morphology (figure 7). In some cases they confirmed some long-held hypotheses of relationships based on morphological evidence, but in other cases the answers they provide have been novel and unexpected. Such is the case with the fundamental question of the identity of the basal clade of parrots.

These new molecular phylogenies were unanimous in pointing toward an unexpected clade as the sister group to the rest of the parrots. Instead of the cockatoos long favored by classical systematists, these new phylogenies identified a clade composed of some of the oddest parrots in the whole family tree: the New Zealand endemics the Kakapo (*Strigops habroptilus*), the Kea (*Nestor notabilis*), and the Kakas (*Nestor meridionalis* and the extinct *N. productus*). The Kakapo will be familiar to many readers as the largest, and for many years the most endangered, of all parrots. It is also one of the strangest, as it is completely flightless, and nocturnal, and has an unusual polygynous lek mating system, in which males advertise loudly to attract females to mating and females are responsible for all subsequent care of the chicks. As we will see in chapter 5, this mating system is definitely the exception to the general pattern of monogamy seen across the parrots. The Kea and Kakas have their own peculiarities (chapter 6). The Kea is one of relatively few parrots to be found at high altitudes, where it has adapted to the limited resources of the alpine zone by evolving a highly omnivorous diet and an unusual degree of curiosity and manipulative intelligence that sometimes sets it at odds with the human inhabitants of these regions (figure 8). The Kaka, which inhabits lower-elevation forests, is also distinctly omnivorous, feeding on fruits, nuts, berries, flowers, nectar, and small invertebrates. Kea and Kakas share extra-long and slim upper bills and tongues tipped with brushy papillae, both of which may be adaptations for extracting sap from trees (chapter 2). Neither of these species is in any way primitive; rather, they exhibit a series of advanced specializations evolved during the long isolation of New Zealand that help them exploit the unusual ecological niches presented by the historical absence of mammals. As a result, they are not thought to closely resemble the ancestral parrot that gave rise to all species that exist today. They are, however, the most basal clade of parrots, and as such are most distantly related to all other parrots alive today.

Other Major Groups of Parrots

Figure 7 illustrates a consensus phylogeny of the parrots built by combining the various molecular studies discussed above. To simplify the patterns of relatedness among major groups, I have combined closely related parrot genera into clades, represented by large triangles, which generally correspond to different families or subfamilies. So each triangle represents a group of species, all of which share a common ancestor with each other more recently than with any other such group. While these triangles simplify the visualization of the large groups they do obscure the relationships among genera within these groups. For details on these relationships I refer interested readers to the resources listed in the notes to this chapter.

To determine the pattern of relatedness among these groups we need to look far back in time at the base of the tree, on the left of figure 7, and then work our way through the branching pattern toward the modern parrots represented by the genera on the right side of

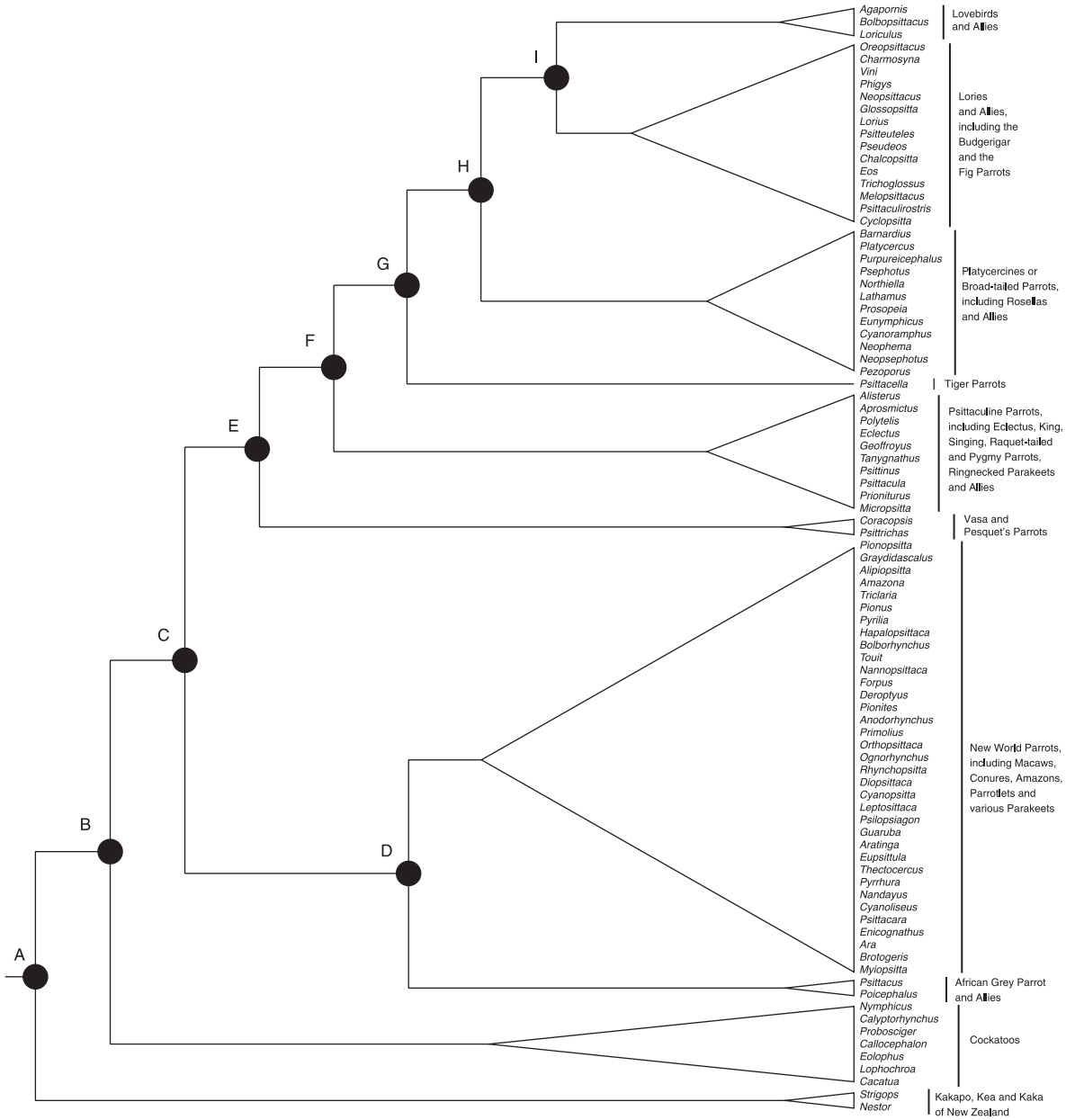


FIGURE 7 Phylogenetic tree illustrating evolutionary relationships among major clades of the parrots.

FIGURE 8 A Kea, *Nestor notabilis,* on rocky outcropping in New Zealand.

the figure. The point at which the peculiar New Zealand parrots diverged from the common ancestor of all the extant parrots is marked as *A* on the far left of figure 7. When we follow the upper branch that leads to the rest of the parrots, we find that the next group to split from their common ancestor (*B*) is the cockatoos. So although cockatoos turn out not to be the most basal clade of parrots, they did diverge quite far back in the parrot family tree and are thus only distantly related to the remaining parrots on the tree.

As we continue to trace our path toward the present, the next branching point (*C*) indicates a split between two major groups of parrots. The lower branch leads to two groups: one an enormous assemblage of all New World parrots (i.e. those that live in North or South America), and the other a smaller group composed of two African genera (*Psittacus* and *Poicephalus)*. The New World clade includes some 150 species of amazons, macaws, conures, parrots, parrotlets, and parakeets. It also includes the extinct Carolina Parakeet, a species whose newly discovered evolutionary relationships are described in box 1. The phylogeny clearly indicates that the enormous diversity of parrots found in the New World all evolved from a single common ancestor that first colonized the Americas, without any further colonization by other lineages of parrots. It also indicates that this ancestor diverged from a common ancestor (*D* in figure 7) that eventually also gave rise to the African Grey Parrot and its smaller *Poicephalus* relatives found only in Africa. Notably, this African lineage did not diversify to the same extent as the one that colonized the Americas, nor, as we will see, was it the only one to invade the continent of Africa.

BOX 1 ANCIENT DNA REVEALS THE EVOLUTIONARY RELATIONSHIPS OF THE CAROLINA PARAKEET

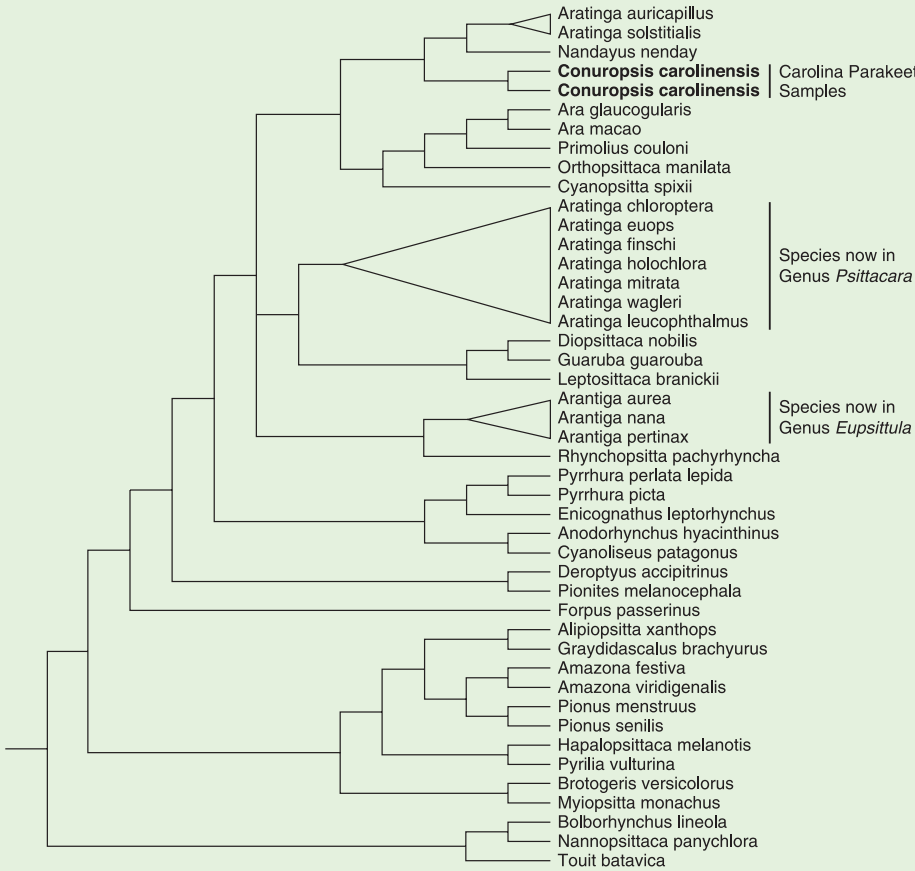
One of the biggest thrills of uncovering the true phylogeny of the parrots has been learning where the Carolina Parakeet *Conuropsis carolinensis* fits into the parrot tree of life. This species became extinct over ninety years ago, well before any systematic study of its ecology, life history or behavior could be undertaken. Even the causes of its extinction remain mysterious; as we will see in the epilogue, many parrot species have become endangered, but most of these occur on islands. In contrast, the Carolina Parakeet was widespread and relatively common over most of the eastern United States before it underwent rapid range contraction and eventual extinction. Even the evolutionary relationships of this lone North American parrot were uncertain. Various candidate groupings had been proposed based on biogeography, plumage coloration, and behavioral adaptations to cold climates. There was a general sense that the closest relatives were probably conures from the genus *Aratinga,* but exactly which species within this large genus was uncertain, to say the least. Recently Jeremy Kirchman, Erin Schirtzinger, and I set out to find the closest relatives of the Carolina Parakeet as a first step toward a better understanding of this enigmatic species.

To accomplish this we first had to overcome a technical challenge: finding usable samples for DNA-based comparisons with existing species. To meet this challenge, Jeremy extracted ancient DNA from the toepads of scientific specimens of the Carolina Parakeet preserved in museums as study skins. He did this work in a lab dedicated to this task that is kept clean of any potential contaminating DNA from more modern specimens. We then used the polymerase chain reaction to make many copies of short fragments of the mitochondrial genome, a small DNA genome exclusive to the mitochondria. Since most cells have many copies of this organelle, mitochondrial DNA is found in relative abundance, even in older specimens where most of the nuclear DNA has been degraded. We then compared the sequences of the Carolina Parakeet to those we had amplified for a broad sample of other Neotropical parrots. With these data we were able to place this extinct species in its rightful spot in the parrot evolutionary tree (box figure 1.1). The results provided new insight not just into the relationships of the Carolina Parakeet but also into general relationships in Neotropical parrots, especially the large assemblage of species once placed in the genus *Aratinga*.

Unsurprisingly, the Carolina Parakeet was placed with confidence in the broader group of Neotropical parrots, reaffirming that all Neotropical species descended from a single common ancestor. Within this group, we found that the Carolina Parakeet was part of a clade that included the Nanday Conure (*Nandayus nenday*) and two

(continued on next page)

(Ancient DNA Reveals the Evolutionary Relationships of the Carolina Parakeet, continued)



BOX FIGURE 1.1. A phylogeny illustrating the relationship of the extinct Carolina Parakeet, *Conuropsis carolinensis,* to other Neotropical parrots. This evolutionary tree also shows that several species classified at that time in the genus *Aratinga* are not each other's closest relatives; some of these species have now been reclassified into other genera.

species of the genus *Aratinga,* the Sun Conure *A. solstitialis* and the Golden-capped Conure *A. auricapillus*. The latter two species, along with another likely member of this clade, the Jandaya Conure *A. jandaya,* all share to varying degrees the distinctive trait of bright yellow and orange plumage on the head, neck, and chest. The other member of this clade, the Nanday Conure, lacks this yellow coloration and instead has a black plumage on its head that may be produced with a pigment that bears some biochemical relationship to the yellow seen in its relatives. All of these species share a distinctive blue edging to their primary and secondary feathers. Thus, in retrospect, plumage provides a strong indicator of the close relationships between the Carolina

Parakeet and other members of this group. In contrast, biogeographical relationships were a poor guide, as other members of this new group are spread from northern Argentina through the Amazon Basin, but none have ranges anywhere near the former range of the Carolina Parakeet. How this species came to occupy its unique range in eastern North America remains a mystery.

Another unexpected finding in our results was that the genus *Aratinga* was not a natural assemblage of closely related species. Instead, our tree indicated that it was composed of at least three different groups, each of which was more closely related to other genera of parrots than they were to other members of their same genus. In addition to the species that grouped with the Carolina Parakeet, there was one clade that included the Brown-throated Conure *A. pertinax,* the Peach-fronted Conure *A. aurea,* and the Olive-throated Conure *A. nana,* and was most closely related to the Thick-billed Parrot *Rhynchopsitta pachyrhyncha* of northern Mexico. Another clade of *Aratinga* was composed of a number of species, including the Mitred Conure *A. mitrata,* Finsch's Conure *A. finschi,* and the Green Conure *A. holochlora,* and was most closely related to a collection of macaws and conures placed in other genera. Again, plumage patterns appeared to be a reasonable guide to distinguishing among these groups, with the Brown-throated Conure clade all sharing olive or brown plumage on their throats or breasts, while most members of the Mitred Conure clade share predominantly green plumage with occasional small patches of red. In contrast, biogeographical patterns were a poor guide, with both clades having members ranging from Central America and the Caribbean down through the Amazon Basin.

In a separate effort led by Van Remsen of the Louisiana State University Museum of Natural Sciences, my colleagues and I set out to realign the old taxonomy of these species with the new reality of parrot relationships. With taxonomic rules dictating that the Sun Conure and relatives remain in the genus *Aratinga,* we moved the Brown-throated Conure and relatives into the new genus *Eupsittula,* and the Mitred Conure and relatives into the new genus *Psittacara.* Other evidence suggests that yet another species, the Blue–crowned Conure *A. acuticaudata,* belongs in its own new genus, *Thectocercus.* While such taxonomic revisions certainly can be a hassle for people accustomed to the previous names, the pain of change is offset by the pleasure of having scientific names that accurately reflect the current knowledge of evolutionary relationships. Bad taxonomy can obscure interesting evolutionary patterns, while good taxonomy can highlight previously unappreciated ones, as with the shared plumage of the Carolina Parakeet and its newly identified relatives.

If we now trace the upper branch leading from *C* we come to the point *E* at which another group of peculiar parrots branches off. These are Pesquet's Parrot (*Psittrichas fulgidas*), found in New Guinea, and the Vasa and Black Parrots of the genus *Coracopsis*, found on Madagascar and neighboring islands off mainland Africa. These two genera are found on opposite sides of the Indian Ocean and bear few resemblances to each other, or indeed to most other parrots. Their relatively close relationship was never suspected before molecular studies. Even now the molecular studies to date have disagreed on how closely they are related and where they fit on the parrot tree, so their placement here in this consensus phylogeny should be considered provisional and, given their geographic remoteness from each other, somewhat of a mystery.

The upper branch leading from *E* leads to several other major groups of birds that comprise the remainder of the parrots. The first to diverge from the common ancestor, indicated by *F* in figure 7, is a diverse group collectively called the psittaculine parrots that includes such well-known parrots as the Eclectus Parrot (*Eclectus roratus*), the King Parrots of the genus *Alisterus*, and the parrots of the genus *Tanygnathus,* which have disproportionately large bills (figure 9). Collectively, this group has one of the broadest geographic ranges of any clade, with representatives spreading from southern Australia through the island archipelagos of Southeast Asia and across India. It also includes one of the most widespread of all parrot species, the Rose-ringed Parrot (*Psittacula krameri*), which has natural populations across the Sahel of Africa and the Indian subcontinent and has established invasive populations in over thirty-five countries outside its native range.

If we take the upper branch from ancestor *F* we come to a branching (*G*) that leads to a small group of four species known as the tiger parrots (genus *Psittacella*), found in northern Australia and New Guinea. The next group to split off (*H*) is a speciose group known as the platycercine or broad-tailed parrots, best characterized by the familiar rosellas (genus *Platycercus*), which are distributed in a rainbow of contrastingly colored species across Australia. It also includes the highly cryptic ground-dwelling parrots of the genus *Pezoporus,* one of which, the Night Parrot (*Pezoporus occidentalis*), is so rare that many thought it extinct through most of the twentieth century until a road-killed carcass was found in 1990 in Queensland, Australia. Most of the other platycercines also are found in Australia, but the species in the genera *Cyanoramphus* and *Eunymphicus* have dispersed as far as the islands of New Zealand, New Caledonia, and Tahiti.

Our final branching point (*I*) is the common ancestor between two other groups that both contain relatives that were not recognized as such until united by molecular studies. One is the large group that is dominated by a peculiar group of birds known as the lories or lorikeets but also includes the well-known Budgerigar (*Melopsittacus undulatus*) and the fig parrots in the genera *Psittaculirostris* and *Cyclopsitta*. We discuss the evolutionary implications of this odd grouping below. In addition to having spectacularly varied plumage and unusual brush-tipped tongues, the lories rival the psittaculines in their ability to colonize distant lands. From their likely origins in New Guinea they have colonized south into Australia, west into Sulawesi and Bali, north into the Philippines, and

FIGURE 9 Great-billed Parrots, *Tanygnathus megalorynchos,* in Indonesia.

far eastward into the Pacific Ocean to settle the remote islands of Fiji, Tahiti, and the Marquesas.

The final group of parrots branching off from ancestor *I* is another group that was only recognized as such through molecular data. It is a smaller group that contains the lovebirds of the genus *Agapornis,* the hanging parrots of the genus *Loriculus,* and the Guaiabero *Bolbopsittacus lunulatus*. It is a geographically disparate group, lovebirds being found across Africa, the Guaiabero restricted to the Philippines, and the hanging parrots stretching between them from India to the Philippines and south into the islands of Indonesia and even New Guinea. Despite this geographic disconnect, the group does share a physical homogeneity, with small, stocky bodies and unusually short tails.

Though the new molecular phylogenies of the past decade have greatly clarified relationships among the parrots, some areas of uncertainty remain. One example of this is the cockatoos, and in particular the relationships of two of the most familiar species, the Cockatiel *Nymphicus hollandicus* (figure 10) and the Palm Cockatoo *Probosciger aterrimus*. The first to address relationships among cockatoos using genetic approaches was a pioneering study published in 1999 by Cathy Toft, the primary author of this book, and her student David Brown. They isolated a short stretch of a single gene of mitochondrial DNA from the small standalone genome of the mitochondria, an organelle found in the cells of all animals (and plants and fungi, too). Mitochondrial DNA has been a popular target for molecular studies, in part because many tissues have multiple mitochondria in each cell, making it easy to isolate high

FIGURE 10 A Cockatiel, *Nymphicus hollandicus,* one of the members of the cockatoo clade.

concentrations of its DNA, and in part because the markers used to target specific genes in one species are often found in other species. Using differences in the basic sequence of this one gene, Brown and Toft reconstructed relationships among the cockatoos. They argued that the Palm Cockatoo was the most basal lineage in the cockatoo family tree, and that the next lineage to split off was a clade containing the Cockatiel, the Gang-Gang Cockatoo *Callocephalon fimbriatum*, and the "black cockatoos" (species in the genus *Calyptorhynchus*). The remaining clades were composed of the "white cockatoos" of the genus *Cacatua* and the Galah *Eolophus roseicapilla*. So, in this early molecular tree the grey Cockatiel was most closely related to a clade composed of the black cockatoos and one of the grey species, while

the black Palm Cockatoo, in its basal position, was most distantly related to all other cockatoo species.

A decade later my colleagues and I revisited the issue using additional evidence as part of our larger study of the relationships amo ng parrot genera. We used a somewhat larger dataset, with two different mitochondrial genes and three stretches of DNA from the nuclear genome that comprises most of our DNA complement. We found somewhat different relationships among the cockatoos, in which the Cockatiel was in the most basal position and with the black cockatoos of *Calyptorhynchus,* the Palm Cockatoo, and then the white cockatoos splitting off in succession. But different analyses of our dataset using different tree-building algorithms revealed some uncertainty in these relationships, suggesting there was more work to be done.

The latest word on this subject is provided by a 2011 study by Nicole White and colleagues from Australia, the land of cockatoos. They undertook to sequence the entire genome of the mitochondria for six cockatoo species plus a subset of genes for most of the rest of the cockatoos. With this massive dataset in hand they had another go at reconstructing cockatoo evolutionary history (figure 11). Their results firmly supported our previous tentative placement of the Cockatiel in the most basal position in the cockatoo family tree, with the black cockatoos next to branch off, and the Palm Cockatoo now sister to a clade composed of the Gang-Gang Cockatoo, the Galah, and the white cockatoos of *Cacatua*. This well-supported arrangement has some interesting implications for some of the physical features of cockatoos. It suggests that the relatively immobile crest of the Cockatiel is ancestral in the cockatoos, and that the fully erectile crest found in the rest of the cockatoos evolved after this lineage split from the common ancestor with the cockatiels. It also suggests that traits such as the black plumage and slender bill shared between the Palm Cockatoo and some other cockatoos have evolved multiple times within different lineages, an evolutionary pattern that we will return to below.

How and When the Parrots Diversified

Throughout this discussion of the past evolutionary history of parrots we have ignored some of the most basic contextual questions, namely when, where, and how the parrots diversified from a single common ancestral species to the over 360 species that exist today. Here again we encounter a larger debate in avian systematics, this one regarding which evolutionary processes led to the diversification of Neoaves and exactly when this diversification took place. It is a vigorous debate, in which the challenge is to marry the evidence from the fossil record with results from modern molecular phylogenies and additional insights from patterns of biogeographic distributions. And once again the parrots are right in the thick of it.

The heart of the debate lies with the question of whether the major clades of modern birds diversified before or after the extinction of their dinosaur relatives 65 million years ago at the boundary between the Cretaceous and the Paleogene periods. In an influential series of books and papers published from the mid-1990s to the mid-2000s, Alan Feduccia of Yale

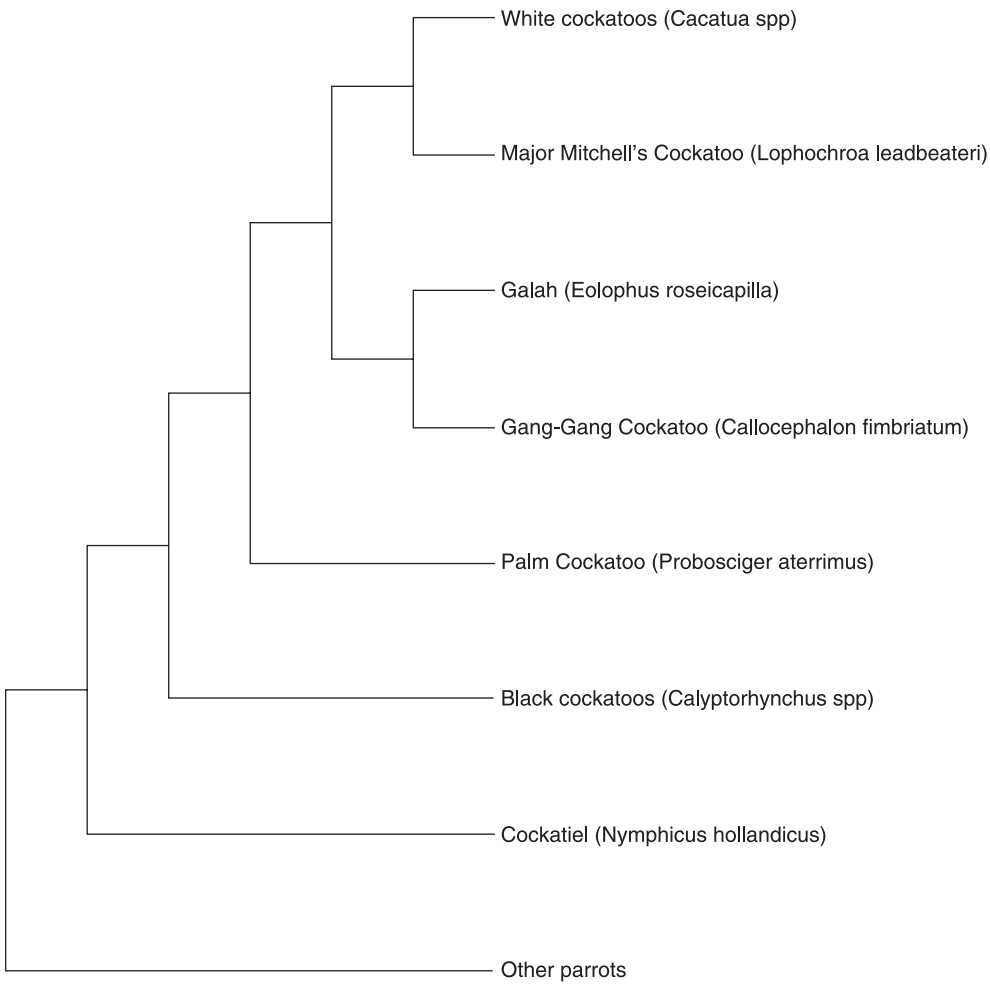


FIGURE 11 A phylogenetic tree of the cockatoos.

University argued that this extinction provided an ecological opportunity that was exploited by the ancestors of modern birds. It resulted in a rapid radiation in which different populations of an ancestral bird adapted to the many different ecological niches left open by the loss of the dinosaurs, and rapidly differentiated into the diverse array of species and body forms now seen among the Neoaves. To support his hypotheses of an explosive radiation, Feduccia relied strongly on evidence from the fossil record, which at that time showed few examples of easily recognizable modern birds from earlier than the K/Pg (K/T) boundary.

A very different conclusion was arrived at by some of the molecular systematists who were then coming on the scene. In 1997, Alan Cooper of Victoria University and David Penny of Massey University used an approach termed *molecular dating* to estimate the timing of divergences among different groups of birds. Molecular dating relies on the

assumption that stretches of DNA accumulate mutations from generation to generation at a relatively constant rate across time and across different evolutionary lineages. If this assumption holds, then the degree of genetic divergence between two species is proportional to the amount of time since those two species diverged and started accumulating mutations independently. If these genetic distances can be calibrated from one or more known points of divergence based on well-dated fossils or geological events, then they can be used as a "molecular clock" to date other divergences in the same tree. Cooper and Penny used a molecular clock calibrated with the oldest fossils known for seven orders of birds and concluded that most of the modern orders of birds had diverged well before the end of the Cretaceous period, perhaps as far back as 100 million years ago. Numerous other studies followed that used similar approaches with different molecular datasets and fossil calibrations. They generally agreed with Cooper and Penny in placing the diversification of modern birds well back in the Cretaceous, although perhaps not so far back as the original study. The gulf between fossil evidence and molecular evidence, although narrowing, remained.

A new take on this controversy was provided in 2001 by Joel Cracraft of the American Museum of Natural History. Cracraft employed an approach termed *historical biogeography* in which he examined the geographic distribution of different groups of birds across different regions of the earth, and aligned the branching patterns in their phylogeny with the known geologic history of these regions. The main conclusions from his work were that many of the major groups of birds showed a pattern of distribution across the continents consistent with an evolutionary origin in the ancient continent of Gondwana. This supercontinent once contained most of the modern continents and landforms now found in the Southern Hemisphere, including Antarctica, South America, Africa, Madagascar, Australia, the Arabian Peninsula, and the Indian subcontinent. It formed about 500 million years ago and broke up gradually, first with the separation of South America and Africa about 100 million years ago. It ended with the final separation of South America and Antarctica about 30 million years ago. Since many of these bird groups were found on several parts of what was once a cohesive supercontinent, Cracraft concluded that they had originated in Gondwana in the Cretaceous and diversified as different populations became isolated from each other by the separation of the continents, a process known as *vicariance*. While this seemed like convincing evidence to many, others were quick to point out that it assumed that these ancestral birds would be unable to disperse from one continent to another, an assumption that seems shaky given the evident ability of many (but not all) modern birds to fly long distances. And so the debate as to when and where the birds diversified continued.

The parrots have figured prominently in this ongoing debate, and they have been cited by both sides as providing support for their arguments. The current fossil record of parrots suggests a later, Paleogene diversification, as the earliest fossils showing clear affinities to modern parrots that have been found to date are in deposits dated to about 50 million years ago, in the Eocene epoch. Studies employing the molecular dating approach, however, have generally placed the initial divergence of parrots from their relatives at a much earlier time in the Cretaceous. Cracraft cited parrots as a prime example of a group with a Gondwanan

distribution because the bulk of parrot diversity is found in South America, Africa, and especially Australasia (meaning the great island archipelagos of Southeast Asia, New Guinea, and Australia). Thus in the parrots, as with birds in general, there existed alternative, and strongly divergent, hypotheses for when the major diversifications took place.

This was the state of the science in the mid-2000s, as my collaborators and I were preparing our first paper on parrot molecular systematics. We were interested in using our new phylogeny, which was the most comprehensive to date, to address the question of when and where parrots diversified. Since both sides of the debate seemed to have valid evidence, and we didn't have strong *a priori* reasons to prefer one side over the other, we decided to test both alternative hypotheses, the one of an ancient Cretaceous divergence and the other of a more recent Paleogene divergence. We tested these hypotheses by using two alternative calibration points for the time at which the most basal lineage split from the rest of the parrots (*A* in figure 7) and then evaluating how well the resulting divergence patterns matched what was known about the geologic history of the continents over the same time frame. In essence, we applied the biogeographic approach of Cracraft to evaluate two alternative hypotheses. We tested the Cretaceous scenario by calibrating the split between the basal New Zealand clade and the rest of the parrots at 82 million years ago, which corresponds to when the islands of New Zealand are thought to have first commenced their protracted split from Gondwana. We tested the Paleogene scenario by calibrating the same split at 50 million years ago, corresponding to the dating of the oldest known parrot fossils, found in Eocene deposits in Europe. We then used the molecular dating approach to estimate divergence times across the rest of our parrot phylogeny.

The resulting "chronograms" suggested very different scenarios for how parrots diversified. The older calibration point gave us a pattern of diversification, the timing of which matched fairly well with geologic events such as the initial separation of Australia from New Guinea and East Antarctica, the separation of South America from West Antarctica, and the relatively recent close approaches of Australia to New Guinea and both of these to Southeast Asia. This scenario suggests that after an origin in Australia, the major splits among modern parrot lineages were due to vicariance, that is, physical separation of populations as the daughter continents of Gondwana broke apart. Subsequent diversification at the level of species or genera occurred within these different continents, perhaps driven by habitat changes caused by global alterations in temperature and sea level.

The more recent calibration told a different story. It also suggests that modern parrots diversified largely in Australia and New Guinea, but only 40 million years ago, perhaps after colonization from the northern continent of Laurasia, where most of the older parrot fossils are found. Colonization of different regions like Africa and South America must then have occurred through dispersal across the oceans separating the continents, with subsequent diversification driven by habitat changes. Overall, we considered this scenario less likely than that suggested by the more ancient divergence, although both were plausible.

Additional insight into the evolutionary diversification of parrots was subsequently provided by Manuel Schweizer in a series of papers in which he too reconstructed phylogenies

of parrots using a different set of genes. He calibrated the divergences within the parrot evolutionary tree by coupling divergence dates derived from fossils of non-parrot bird groups that have richer fossil histories than parrots with phylogenies of the relationships of parrots with these groups. This approach allowed him to estimate the timing of divergences with much greater confidence than our single parrot fossil approach. The resulting time-calibrated trees (chronograms) were much more closely aligned with our second scenario, a later divergence in the Eocene. They provided strong support for the idea that many of the modern lineages of parrots became established in their current locations through an active process of over-sea dispersal, rather than a passive riding of different continental blocks as they split apart. The debate could be reignited by the discovery of a single parrot fossil from the Cretaceous, perhaps in a little-explored area like Antarctica, which was once much warmer and more welcoming to parrots. At present, though, the weight of the evidence suggests that the initial divergence of the modern parrots occurred in the Australo-Papuan region about 58 million years ago in the Eocene, and was followed by the colonization of South America, Madagascar, and Africa by dispersal over oceans.

With the stage now set for where and when the parrots diversified, I will focus for the remainder of the chapter on a few specific questions, about specific branches of the parrot family tree, that illustrate some interesting general principles concerning the winding paths taken by evolution.

SOME PARROT ENIGMAS

What Is a Budgerigar?

In some senses the question "What is a Budgerigar?" is immediately answerable. It is the most popular captive parrot species in the world. This small parakeet is native to the interior of Australia. There it roams widely, often in large flocks, breeding opportunistically when the intermittent rains of that dry land fall sufficiently long and hard to produce enough of its favored grass seeds to sustain a clutch of chicks. The Budgerigar was first described as a species in 1805 by George Shaw, and the first live bird was brought to Europe in 1840 by noted ornithologist John Gould. Shortly thereafter aviculturists began breeding Budgerigars in captivity. The birds proved readily adaptable to captive life and quickly grew to enjoy the wide popularity as pets that they still enjoy today. This popularity can be attributed to their playful personalities, intelligence, relatively mellifluous voice (for a parrot), and dazzling assortment of color varieties. These last have been bred by aviculturists, who carefully selected any mutations that diverged from the wild-type coloring of yellow face, brilliant green breast and belly, and mottled black-and-yellow head that verges into a scalloped yellow-and-black pattern on the back. It is this scalloped patterning that gives rise to another name for the Budgerigar, the shell parakeet. The origins of the name "Budgerigar" are unknown but are thought to derive from corruptions of a name used by Aboriginal inhabitants of Australia.

The small size and adaptable nature of the Budgerigar have also made it popular as a subject for scientific studies. As will be discussed in later chapters, a substantial amount of

what we know about such diverse topics as how parrots feed their young, how the brilliant colors in parrots feathers are formed, and how parrots produce, learn, and perceive their varied communication calls have come from studies of captive Budgerigars. Paradoxically, the life of wild Budgerigars remains relatively unstudied, apart from the pioneering studies by Ed Wyndham and a few other intrepid Australian ornithologists (see chapter 6). This paradox arises from the nomadic nature of Budgerigars, which makes sustained study of the same populations well-nigh impossible. The difficulties are compounded by the enormous flock sizes that are sometimes seen—just imagine the difficulty in following the movements of one marked bird within the kaleidoscopic whirl of a flock of thousands as they fly across the scrublands of Australia (figure 12).

Until recently our ignorance of the wild Budgerigar extended even to the fundamental question posed at the beginning of this section: What is a Budgerigar? Or, to state it in evolutionary terms, where does this species fit in the parrot Tree of Life, and who are its closest relatives? For many years this question was approached in the same way all of parrot systematics was approached: by comparing anatomical, morphological, and behavioral characters, adding in considerations of geographical distributions, and making considered judgments as to which species most closely resembled each other and were thus most closely related. The conclusion that was drawn by early workers in parrot systematics was that the Budgerigar was part of a collection of parrots with long wings and long, broad tails collectively known as the platycercines that, as we have seen, is distributed across Australia and neighboring islands. As described above, other parrots historically thought to be in the Platycercines include the brightly colored rosellas of the genus *Platycercus,* the migratory swift parrot *Lathamus discolor,* the widely distributed parakeets in the closely related genera *Eunymphicus* and C*yanoramphus* that are found on New Zealand and the far-flung islands of the southern Pacific Ocean, and the ground-dwelling parrots of the Genus *Pezoporus* (figure 13). In particular, the latter were judged to be the closest relatives to the Budgerigar given their similar mottled green-and-yellow plumage, their shared habit of feeding on the ground, and their overlapping distributions in the arid interior of Australia.

This picture changed, however, when scientists started using DNA evidence to reconstruct the evolutionary history of parrots. In a study published in 1991, Les Christidis and colleagues included the Budgerigar in a phylogenetic study based on variation in allozymes, or protein variants. Their work suggested that Budgerigars are most closely related to lorikeets, a relationship so novel that the authors were inclined to dismiss it as an experimental artifact. The first DNA-based study to include Budgerigars was the pioneering study by de Kloet and de Kloet discussed above. Their phylogenetic trees, built with sequences from the sex-linked spindlin genes, confirmed the close evolutionary relationship between the Budgerigar and the lorikeets, extensive differences between lorikeets and the Budgerigar in diet, habitat, and appearance notwithstanding (figure 14). This new grouping was later supported by our study that included wider sampling of different parrot groups and genes, by subsequent studies by Manuel Schweizer and colleagues, and by Gerald Mayr's anatomical studies. Support is now robust for the hypothesis that the Budgerigar is the closest relative of the lorikeets and that

FIGURE 12 A superflock of Budgerigars, *Melopsittacus undulatus,* in their native grasslands near the Karratha area, Australia.

FIGURE 13 A Western Ground Parrot, *Pezoporus wallicus flaviventris*.

FIGURE 14 An endangered Red-and-Blue Lorikeet, *Eos histrio,* from the Talaud Islands, Indonesia.

both belong in a broader clade that also includes the fig parrots of the genera *Cyclopsitta* and *Psittaculirostris*. This firmly established relationship puts a novel twist on thinking about the evolution of the lorikeets themselves, and in particular how the unusual lifestyle of nectarivory (feeding on nectar), and its anatomical peculiarities like brush tongues, evolved from the seed-eating habits of the Budgerigar and fig parrots. In chapter 2 we will examine in more detail this lifestyle and the consequences it has for lorikeet anatomy and physiology. As a final addendum, a later study I conducted with Leo Joseph and colleagues showed that the ground parrots of genus *Pezoporus* that were formerly linked with Budgerigars were most closely related to the grass parrots in the genera *Neophema* and *Neopsephotus,* all of which live in Australia and some of which are brightly colored with patches of blue, orange, pink or yellow. It appears that the mottled green-and-yellow plumage seen in both the ground parrots and the Budgerigar is not a trait derived from a shared common ancestor, as formerly thought, but instead a product of convergent evolution driven by similar selective pressures imposed by their shared lifestyle of feeding on the ground and the need for cryptic plumage that helps them blend into the grasses and hide from aerial predators.

How Have Different Body Shapes Evolved in the Parrots?

Anyone who has paged through Joseph Forshaw and William Cooper's masterpiece *Parrots of the World* or another book illustrating parrot diversity will immediately notice the immense variety among the species. Each species differs from all others, whether it is the

arrangement of its brilliant plumage patches, the color or shape of its bill, the size and shape of its wings, the overall size of its body, or some unique combination of all these attributes. Continue paging through the book, however, and you will begin to notice that some features are shared across multiple species. Cockatoos have erectile crests. Some of them have white plumage, while others have black or grey. Lorikeets have brushy tongues with many raised papillae. Macaws of the genera *Anodorhynchus* and *Ara* have particularly massive bills, even given their large body size. Several species in the neotropical genus *Aratinga* have brilliant golden plumage on their head or bodies, while all of the species in the genus *Prioniturus* found in the islands of Southeast Asia have distinctive racquet tails, in which the two elongated central tail fathers have extended shafts that are bare but for tufts of feather barbs at the tips. The list of such shared characteristics becomes longer and longer as one continues to examine the book.

The question of why two different species might share a given trait is a fundamental one in evolutionary biology. At its most basic, there are three alternatives for such shared similarities. One is that the species in question are closely related, and share the trait because at some point in the evolutionary past their common ancestor had the same trait. A trait that is shared between species due to their shared ancestry is called a *homologous* trait. A likely example of such a trait is the erectile crest of the cockatoos, since all members of the group except the most basal species, the Cockatiel, share the trait and the cockatoos are well supported as a cohesive group in a variety of studies, as described above. In other cases, two species may look similar because similar selective pressures have promoted the evolution of similar traits *de novo* in each species. Traits that arise from shared selective pressures but are not present in the common ancestor are called *analogous* or *convergent,* and the process that produces them is called *convergent evolution*. A likely example of convergent evolution is the cryptic plumage of the Budgerigar and the *Pezoporus* parrots described above, which is not due to shared ancestry (they are not closely related to each other) but instead may result from natural selection working on both species to reduce their visibility while feeding on the ground. Similar selection may have been at work on the ancestors of the ground-dwelling Kakapo of New Zealand to produce their mottled brown-and-green plumage; although mammalian predators are absent from New Zealand there is abundant fossil evidence of avian predators that became extinct following the arrival of the Maori. A third possibility is that the trait was present in an ancestor further back in the tree. Hummingbirds and parrots, for example, both have feathers not because they share a more recent common ancestor with each other than either does with any other bird group, but because all birds have feathers.

Importantly, a trait's being homologous and shared by close relatives does not mean it is without adaptive value for the species that have it; traits present in an ancestor may be maintained through natural selection in descendent species because they confer a benefit to these species. Conversely, as our ability to uncover the genes involved in producing specific traits improves, we are beginning to discover that traits that evolved convergently sometimes are produced by the same genetic variants or collections of genes, which have been

FIGURE 15 Comparison of a Red-cheeked Parrot, *Geoffroyus geoffroyi* (left), and a Red-lored Amazon, *Amazona autumnalis* (right), two distantly related parrot species with similar morphotypes.

independently recruited during natural selection to produce similar traits in distantly related species. Puzzling out the genetic pathways underlying phenotypic traits and determining the extent to which traits are homologous or convergent is one of the most exciting and challenging frontiers in evolutionary biology today.

The body shapes of different parrots present just such an intriguing challenge to evolutionary biologists. Some parrots, like members of the genera *Amazona, Psittacus, Geoffroyus* and *Cacatua,* have stocky bodies, short, square tails, and broad, rounded wings (figure 15). Others, like species in the genera *Forpus* and *Cyclopsitta,* have small bodies with broad pointed wings and short wedge-shaped tails. Still others, like members of *Polytelis* and *Psittacula,* have narrow pointed wings and long narrow pointed tails. As with all birds, such differences in wing, tail, and body shape, sometimes termed *morphotypes,* strongly affect the flying abilities of the birds, with some morphotypes having greater speed and others having greater maneuverability. As such, they can strongly affect the fitness of individuals in a given habitat and are likely the product of natural selection. But to what extent are these morphotypes homologous versus convergent?

One of the first to tackle this question in parrots using modern genetic methods was Cristina Miyaki and members of her research group at the Universidade de São Paulo in Brazil. They investigated the evolutionary relationships among the parrots of the Neotropics

using mitochondrial DNA and found that, broadly speaking, the nine species they sampled fell into two clearly separate clades. One was composed of the Blue-fronted Amazon *Amazona aestiva* and the Blue-headed Parrot *Pionus menstruus*, both species with short tails and broad, rounded wings. The other was composed of the Hyacinth Macaw *Anodorhynchus hyacinthinus,* the Painted Conure *Pyrrhura picta*, the Blue-and-Yellow Macaw *Ara ararauna*, the Golden Conure *Guaruba guarouba*, Spix's Macaw *Cyanopsitta spixii*, and the Hawk-headed Parrot *Deroptyus accipitrinus*. For the most part these species have long, graduated tails and broad, pointed wings. In recognition of the strong concordance between morphotypes of the species sampled and their independently derived evolutionary relationships, Miyaki and colleagues labeled these the short-tailed and long-tailed clades. Subsequently, other studies by Miyaki's group, de Kloet and de Kloet, Schweizer and colleagues, and my own research group have extended this work by sampling more species and more genetic markers, and in the process have created a family tree for the Neotropical parrots that contains nearly all the species. The picture that has emerged has confirmed and amplified on Miyaki's early work. It now appears that these parrots fall into five distinct clades, most of which correspond to a distinct morphotype. In addition to the long-tailed and short-tailed clades described above, there is now thought to be a clade composed of the genus *Brotogeris* and the Monk parakeet *Myiopsitta monachus*, both of which have broad pointed wings and graduated tails of moderate length, and a clade composed solely of the genus *Forpus,* which are small parrots with short, pointed wings and extremely short wedge-shaped tails. The exception to the strong correspondence between morphotypes and phylogenetic clades is a clade composed of the genera *Touit, Nannopsittaca, Bolborhynchus*, and *Psilopsiagon,* most of which have broad, pointed wings but which sport a variety of tail types, from the short squarish tail of the members of *Touit* and *Nannopsittaca* to the long graduated tails seen on the members of *Psilopsiagon*. Such differences may be driven by selection from the different habitats inhabited by these different genera.

Overall, though, the picture that emerges from our improving knowledge of Neotropical parrot evolutionary history is that body shape is fairly conserved within the different clades, such that most species tend to be shaped like closely related species. This pattern provides good evidence that within the Neotropical parrots these morphotypes are homologous traits, derived from ancestors that had similar shapes. A recent paper by Manuel Schweizer and colleagues suggests that the diversification into these different ancestral morphotypes occurred shortly after the common ancestor of all Neotropical parrots colonized the Americas, probably about 30–35 million years ago. This initial colonization was followed by a rapid diversification into the five morphotypes as the ancestral parrot populations adapted to the local conditions they found. These ancestral morphotypes then persisted and further diversified into the more than 150 species we see today as they moved through South and Central America, into the islands of the Antilles, and, in a few cases, into North America.

The picture becomes more complicated, though, when we broaden the scope to look across all parrots. Each of the morphotypes discussed so far has representatives not just in the Neotropics but also in species seen in other parts of the world. For example, the same

stocky bodies, broad rounded wings, and short square tails seen in *Amazona* and *Pionus* in the Neotropics are also seen in the African Grey Parrot *Psittacus erithacus* of Central Africa, the Kea *Nestor notabilis* of New Zealand, and the Galah *Eolophus roseicapillus* of Australia. Yet the clear picture that has emerged in the last decade from phylogenetic analyses of parrots is that these species are all in different evolutionary lineages. This pattern tells us that on a broader scale, similar morphotypes have evolved convergently in different lineages of parrots. Whether similar mutations in the same or different genes that produce these body plans have been promoted by natural selection in different lineages remains an exciting question for future investigation.

Now that the stage is set and the players have been introduced, it is time to move into the main act. In the following chapters we delve deeper into the lives of wild parrots. We start with aspects of physiology and behavior: how different species have adapted to different diets, how parrots perceive the world around them and communicate with others, and how they use their impressive brains to process this information. We will then move on to examine questions of parrot life history: how they find mates, raise their offspring, and live their long lives. We will end with the population biology of parrots, focusing on how populations are affected by the many changes we humans are making in the natural world. Throughout, we will draw on the rich and rapidly growing body of scientific literature that is shedding an ever-greater light on the previously obscure and mysterious lives of parrots in the wild.